

CONVERGENCE IN THE STRUCTURE OF THE
HEAD AND CUTICLE OF *EUCHROMADORA*
SPECIES AND APPARENTLY
SIMILAR NEMATODES



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SYNOPSIS

The comparative anatomy and structure of the head and cuticle is described in several species of *Euchromadora* and a number of other morphologically very similar species in which the cuticle is complex and heterogeneous and the lateral pieces of the gubernaculum are massive and typically L-shaped. *Euchromadora* species are characterized by a solid dorsal onchium, a series of denticles in transverse rows on both the lateral and ventral walls of the oesophastome, a cuticle in which the large punctations are due to the presence of processes arising from one side of each cuticular annule and there are no markings on the cuticle along the dorsal and ventral surfaces over much of the length of the body. Other *Euchromadora*-like species which in the past have been described as having an anteriorly directed dorsal onchium are shown to possess hollow-type dorsal onchia; flanges on the lateral walls of the oesophastome; anteriorly directed, cone-like onchia on the ventral sectors of the oesophastome; a cuticle in which the large punctations are frequently due to processes developed from both sides of each cuticular annule and there are markings on the cuticle of the dorsal and ventral surfaces along the whole length of the body. As a result the following major taxonomic changes are proposed. *Euchromadora* de Man, 1866 retains seven species: *E. vulgaris* (Bastian, 1865), type species of the genus; *E. gaulica* Inglis, 1962; *E. meadi* Wieser & Hopper, 1967; *E. permutabilis* Wieser, 1954; *E. striata* (Eberth, 1863); *E. tokiokai* Wieser, 1955; *E. eileenae* sp. nov. *STEINERIDORA* Gen. Nov. is very similar to *Euchromadora* but has large, sickle-like onchia arising from both the lateral and ventral walls of the oesophastome and a distinct posterior oesophageal bulb. It contains the following four species: *S. loricata* (Steiner, 1916), type species of the genus; *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S. (?) dubia* (Steiner, 1918) *species inquirenda*. In the remaining genera the dorsal onchium is hollow. *Graphonema* Cobb, 1898 is rediagnosed on the basis of Australian specimens which are undoubtedly congeneric with those described by Cobb so that this genus is characterized by a swollen, set-off head, and two circles of cephalic setae. It contains the following species: *G. vulgaris* Cobb, 1898, type species of the genus; *G. georgei* sp. nov.; *G. amokuræ* (Ditlevsen, 1921) Wieser, 1954. The rediagnosis of *Graphonema* displaces species in which the dorsal onchium, although hollow, is controlled by a massive development of the dorsal oesophageal musculature, there is a posterior oesophageal bulb and the gubernaculum is small and not L-shaped. The four species involved are referred to a new genus *Innocuonema*: *I. flaccida* (Wieser, 1959) type species of the genus; *I. clovosa* (Wieser, 1959); *I. dentabunda* (de Man, 1890); *I. chilensis* nom. nov. pro *G. amokuroides* of Wieser, 1954. The discovery of *Nygmatochus alii* Murphy, 1965 led to a reassessment of *Nygmatochus* Cobb in Cobb, 1933 which is considered to contain four species: *N. scriptus* Cobb in Cobb, 1933, type species of the genus; *N. fossiferus* Wieser, 1954; *N. minutus* Gerlach, 1967; *N. bicornata* (Wieser, 1959) comb. nov., in all of which the cuticle is laterally differentiated, the amphid has a prominent double contour and there is a (?) pre-cloacal modification on the male body. *N. alii* is referred to a new genus *Austranema* with three other species: *A. colesi* (Inglis, 1968), type species of the genus; *A. alii* (Murphy, 1965); *A. pectinata* (Weiser & Hopper, 1967); *A. shirleyae* (Coles, 1965), characterized by the possession of a circle of ten cephalic setae, a head which is not set-off and the presence of a median pre-cloacal thickening on the ventral surface of the males. A new genus and species, *Parapinnanema wilsoni*, is described in which the cuticle is very thick and obviously battlement-like, the dorsal onchium is hollow and the lateral flanges of the oesophastome are not dentate anteriorly, the cephalic sense organs are in three circles of which the intermediate and outer are setae and there is a region of pre-cloacal modification on the males. Finally a new genus, *Protochromadora*, is proposed for three species: *P. scampae* (Coles, 1965), type species of the genus; *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958), in which there are no structures on the lateral walls of the oesophastome, the cuticle lacks punctations on the dorsal and ventral surface and there is no pre-cloacal modification on the ventral surface of the male. Five species are described from the coasts of Western Australia, thus: *Euchromadora striata* (Eberth, 1863); *E. eileenae* sp. nov.; *Graphonema georgei* sp. nov.; *Parapinnanema wilsoni* gen. et sp. nov.; and *Hypodontolaimus slacksmithi* sp. nov. The classification of the Chromadoridae is briefly discussed in view of the recognition that complex cuticle,

structure of the dorsal onchium, form and distribution of cephalic sense organs and shape of lateral pieces of the gubernaculum are not covariant. Nomenclatural changes are listed on page 201.

INTRODUCTION

THE classification of the nematode family Chromadoridae Filipjev, 1917 is largely based upon the appearance of the cuticle and its associated lateral differentiation, the shape of the amphids and the gross form of the dorsal onchium which occurs in the buccal cavity. Thus de Coninck (1965) recognizes three subfamilies within the family: Chromadorinae with a solid dorsal onchium and non-spiral amphids; Hypodontolaiminae de Coninck, 1965 with a hollow dorsal onchium and non-spiral amphids; and Ethmolaiminae Filipjev & Schuurmans Stekhoven, 1941 with a hollow dorsal onchium and spiral amphids. Within each of these subfamilies genera are distinguished very largely by the distribution and form of the cephalic sense organs, the appearance of the cuticle, the presence or absence of lateral differentiation and the dentition of the buccal cavity.

Using such criteria the genus *Euchromadora* de Man, 1886 is apparently easily recognized by a blunt head, a prominent solid dorsal onchium, a characteristically dark and complicated cuticle and a gubernaculum of a unique L-shape. Several authors have drawn attention to the possible value of the detailed structure of the cuticle as a source of taxonomic data within the genus (Steiner & Hoeppli, 1926; Inglis, 1962; Coles, 1965; Wieser & Hopper, 1967) but it has rarely been studied in detail in one species (Steiner & Hoeppli, 1926; Inglis, 1964; Watson, 1965) and never comparatively in a number of species.

The peculiar and characteristic shape of the gubernaculum has generally been well described and appears to supply "One of the most decisive features of this genus . . ." (Wieser, 1954, page 101). However it has never been shown that the characteristic gubernaculum is consistently associated with the elaborate cuticle and the large solid onchium. Some doubt about this assumed covariance is raised by Murphy's (1965) description of *Nygmatochus alii* Murphy, 1965 in which an L-shaped *Euchromadora*-type gubernaculum is associated with a complex cuticle and a hollow dorsal onchium. It will be shown below that this doubt is well justified.

The difference between a hollow and a solid onchium is spectacular and obvious when the extremes of both conditions are compared but intermediate forms occur which I have found difficult, if not impossible, to classify in this way with accuracy. It was, therefore, thought necessary to establish whether the hollow and solid onchia are associated with other more easily distinguished features before accepting this difference as a basis for classification.

The difficulty of distinguishing between the solid and hollow condition has arisen with others in the past since both Wieser (1954) and de Coninck (1965) refer *Spilophorella* Filipjev, 1918 to the solid-onchia group while to me all the illustrations of species referred to that genus, and all the specimens I have studied, are best described as possessing hollow onchia.

Similar confusion has arisen in another way since both Wieser (*loc. cit.*) and de Coninck (*loc. cit.*) group *Odontocricus* Steiner, 1918 and *Dicriconema* Steiner & Hoeppli, 1926, in both of which the cuticle is complex, with those genera in which a solid dorsal onchium is definitely present. This can only have been based on an assump-

tion of covariance between the solid onchium and the complex cuticle since in neither case is any information available about the structure of the dorsal onchium. In *Dicriconema* the illustration of the anterior end of the body given by Steiner & Hoeppli (1926, Pl. 1, fig. 1) suggests that the dorsal onchium is hollow while the uninformative description of *O. hupferi* Steiner, 1918 simply mentions the presence of a dorsal onchium. However this description is preceded by a description of *Euchromadora luederitzi* Steiner, 1918 in which the dorsal onchium is illustrated as hollow.

The unreliability of the gross appearance of the cuticle as an indicator of other similarities is understandable when we recall the functional importance in the Nematoda of a cuticle which is longitudinally flexible while tangentially strong (Inglis, 1964). Attention has already been drawn to the narrow morphological range within which the cuticle could be, or has been, modified (Inglis, 1965) so that it is easy to appreciate that massive convergence in the appearance of the cuticle is more likely to be the rule than the exception. Such convergences are unlikely to be recognized so long as the structure of the cuticle is considered under such simple headings as homogeneous/heterogeneous, simple/complex. However, the complexity of the cuticle in some forms leads to very great difficulties in analysing its structure in any greater detail than is implied by such simple groupings and here again it is necessary, if possible, to establish the co-occurrence of other more easily studied features.

It is clear that, as de Coninck (1965) stresses, the taxonomy of the Family Chromadoridae is in need of examination but it is difficult to see that any such revision can be based upon a reassessment of the kind of information generally available. Too much of the present classification is fortuitous, too many of the groupings recognized are based on bibliographical information and too many of the morphological studies have been carried out with the sole aim of delimiting species. The major difficulties in overcoming this are the time needed to carry out comparative studies and the small size of the specimens involved.

I have been able to carry out some such comparative studies on specimens collected from the coasts of Western Australia. The specimens are in some cases confusingly *Euchromadora*-like in appearance but detailed examination disclosed discrepancies which led me to study such species of the genus *Euchromadora* as were easily available in large numbers. The unexpected results are presented here.

MATERIALS AND METHODS

Almost all the specimens were killed and fixed by gathering seaweed by hand and putting it into plastic bags with seawater. Sufficient formalin was then added to the bags to make a 7% formalin solution. The bags were shaken and nematodes picked out later by hand under a stereoscopic dissecting microscope. Specimens were then studied under a compound microscope; uncleared and mounted in alcohol or cleared and mounted in glycerine (prepared by a slow method involving the evaporation of alcohol from an alcohol: glycerine mixture); or in lactophenol. The structure of the cuticle was examined in squashes, in whole mounts, by transmitted light, by phase contrast and after treatment with sodium hypochlorite. This latter

method produces separate rings of the sclerotized annules and rods of the cuticle. Finally the rings of sclerotized cuticle were studied through crossed polaroid filters when their birefringence makes them stand out spectacularly.

The heads were studied by mounting in glycerine jelly in a few cases but, more commonly, they were mounted in liquid glycerine or lactophenol under cover-slips supported by lens cleaning tissue. This latter method allows the head to be tilted to any angle so that it can be studied in detail. In a few cases it was possible to evert the anterior end of the oesophagus through the mouth opening so that the dentition could be studied in great detail.

All whole mounts were fluid and temporary with the coverslips supported by paper so that it was possible to get a view of the animals from any angle by rolling.

The use of Cobb slides or other form of permanent mount is to be deprecated for morphological studies. Such slides are undoubtedly useful and simple for routine identification but are a grave handicap in establishing the taxonomy of any group of nematodes. The use of any permanent mount leads to the treatment of the animals being examined as two dimensional and to the description of plates, seen in optical section, as rods; to the description of flanges as teeth and to the analysis of solid curved structures as hollow or pierced by holes or channels.

Studies of the kind reported here are generally time consuming and sometimes difficult but experience in other fields of nematology has shown that *en face* views of the head, although not always essential in the delimitation of species, are essential in establishing any meaningful classification above the species level.

Most of the specimens studied were collected from various localities on the coast of Western Australia during October, 1966, but some were collected on the coasts of Europe, particularly the British Isles, and one sample originated from South Africa. The holotype males of all new species are deposited in the collections of the Western Australian Museum, Perth, Western Australia. Paratypes are deposited in the same institution and in the collections of the British Museum (Natural History), London, S.W.7.

Species Studied

Euchromadora adriatica (Von Daday, 1901)

Euchromadora colesi Inglis, 1968

Euchromadora eileenae sp. nov.

Euchromadora gaulica Inglis, 1962.

Euchromadora loricata (Steiner, 1916)

Euchromadora mediterranea Allgén, 1942.

Euchromadora scampae Coles, 1965.

Euchromadora shirleyae Coles, 1965.

Euchromadora striata (Eberth, 1863)

Euchromadora vulgaris (Bastian, 1865).

Graphonema georgei sp. nov.

Hypodontolaimus slacksmithi sp. nov.

Nygmatochus alii Murphy, 1965

Parapinnanema wilsoni gen. et sp. nov.

THE STRUCTURE OF THE HEAD

The head of any nematode is derived developmentally from two sources, from the anterior end of the region of primary embryonic invagination, the stomodaeum, which becomes the oesophagus (there is some reasonable doubt about this interpretation of the oesophagus as a stomodaeum, which is generally overlooked, and the term is used here for convenience) and from a region of secondary overgrowth derived from the hypodermis. These two regions are generally easily distinguished in histological sections because the primary oesophageal region is lined by simple, structurally uniform cuticle while the secondary region is lined by cuticle which is continuous with and similar in appearance to the cuticle covering the outer surface of the body.

The entire mouth cavity of nematodes I have proposed should continue to be called the stoma; the region of secondary overgrowth continues to be known as the cheilostome while any region of specialization at the anterior end of the oesophagus (i.e. region of primary invagination) is the oesophastome (Inglis, 1965; 1967). The wall of the cheilostome is the cheilorhabdion and that of the oesophastome is the oesopharhabdion. Following Cobb's (1919) terminology as modified by Chitwood (1950) I use the term odontium for any tooth-like structure developed from the cheilostome and the term onchium for any similar structure developed from the oesophastome. For convenience the general term denticle will also be used in this paper to imply a small solid cuticular tooth-like structure developed from the oesopharhabdion.

The cheilostome in the Chromadoridae is typically shallow, without odontia but with a circular mouth opening surrounded by twelve rugae. In some cases the terminal processes of the rugae are lacking and there are twelve flange-like supporting structures which project into the cheilostome as curved wedges which may warrant description as odontia (see page 198).

The cuticle covering the anterior end of the body is either without punctations or, more posteriorly, the punctations are simple and rod-like. It is worth noting that when the cuticle in *Euchromadora* is stained with Mallory's Triple Stain this lightly punctate region stains various shades of light blue while the more elaborate punctate component posteriorly stains a dense orange-red. This difference in staining reaction appears to reflect a difference in the degree of sclerotization and flexibility of the cuticle, the blue regions being flexible while the orange-red are relatively rigid (Inglis, 1961).

In *Euchromadora* and similar forms, most of the variation in the structure and elaboration of the anterior end of the body is restricted to the oesophastome, into which a large dorsal onchium almost invariably projects. The oesophastome is in the form of a cup formed by an expansion of the lumen of the oesophagus at its anterior end. The cuticular walls of this oesophastomal cup are thick and prominent and form curved sheets which blanket the cup tangentially. The thickening of the cup extends posteriorly into the true tri-radiate lumen of the oesophagus where it becomes increasingly thin posteriorly until it ceases to be obvious (Text-figs. 3, 19, 43, 46).

The oesophastomal cup is roughly rectangular in transverse section (i.e. when viewed *en face*). The dorso-lateral radii of the oesophagus arise from the dorso-lateral corners of this rectangular cavity while the ventral arm of the lumen arises from the mid-point of the ventral side of the rectangle. The boundaries between the dorsal and lateral walls are, therefore, easily established by the dorso-lateral arms of the oesophageal lumen. The boundaries between the lateral and ventral walls (more correctly sub-walls for uniformity but called walls for convenience) are frequently set-off by somewhat similar ventro-lateral extensions of the lumen of the oesophagus. These extensions can be spectacularly obvious in some species. In all cases, however, the limits can be established not only by the shape of the oesophastome but also by the distribution of the modifications in the form of onchia and plates present on the lateral and ventral walls (Text-figs. 1, 6, 12, 13, 27, 30, 39, 42, 45, 47, 52, 58).

In typical *Euchromadora* species as exemplified by *E. vulgaris*, the type species of the genus, the dorsal wall of the oesophastome is fairly straight, in an *en face* view, and bears a series of wholly cuticular onchia (or denticles) along its anterior edge (Text-figs. 12, 13). Posterior to this level is the large, wholly cuticular onchium which projects into the oesophastome and articulates posteriorly on the thickened dorsal wall of the oesophastome.

The anterior, most dorsal, edge of the lateral walls projects inwards over the cavity of the oesophastome as a pointed, somewhat onchium-like flange which arises from the ventral edge of the dorso-lateral radii of the lumen of the oesophagus. Posterior to this extreme anterior edge the lateral walls bear a series of wholly cuticular, generally tiny, denticles which run roughly dorso-ventrally (i.e. transversely when viewed from the lateral aspect of the body) in distinct rows, of which four can usually be recognized. In some cases one or more of these onchia is larger than the others and the rows may be straight or bent (Text-figs. 2, 17, 24, 34).

The ventral walls of the oesophastome also bear a series of small, wholly cuticular denticles with, usually, a series of much more prominent solid onchia arising from a basal plate low down in the oesophastome or from the border between the ventral walls and the median-ventral extension of the lumen of the oesophagus (Text-figs. 1, 6, 12, 13, 25, 27 etc.).

In all the species in which the dorsal onchium is unequivocally hollow, and in many in which no decision can be easily reached, the conditions are consistently different. The oesophastome is still in the form of a rectangular cup with thickened cuticular walls but the dorsal onchium is not, or not obviously, solid. This means that the musculature controlling it passes into the lumen of the onchium and does not attach to its base as in solid onchia. The anterior edge of the oesophastomal cup, which is generally strongly curved dorsally, is not dentate along its anterior edge, while ventrally and laterally there are no rows of small denticles. Instead two large cone-like cuticular onchia arise from the ventral floor of the oesophastome with, in some species, another smaller similar pair which arises from the edge of the ventral lumen (Text-figs. 30, 39, 42, 45, 52).

The lateral walls of the oesophastome do not bear series of denticles, instead, there is a cuticular flange which stands independent of, but parallel to each lateral

wall (Text-figs. 44, 45, 52, 54). The anterior edge of this flange is generally higher towards the dorsal surface of the body than the ventral and in some species is divided along its anterior edge to produce a series of tooth-like points which project wholly anteriorly. When viewed from the ventral aspect this flange looks like a tooth arising from the lateral wall of the oesophastomal cup (Text-fig. 54; see also Fig. 21 in Coles, 1965). Its shape in *en face* views is very characteristic because it stands free more posteriorly on its ventral edge than it does on its dorsal. This means that when viewed in optical section *en face* it gives the appearance of being a ventrally curved hook-like derivative from the wall of the oesophastome. The shape of this lateral flange and the presence and distribution of the ventral cone-like onchia is shown by Murphy (1965) in his figure of the head of *Nygmatochus alii* (Murphy's Fig. 1, D).

In all species the head bears sixteen cephalic sense organs of which six are arranged in a circle near the edge of the mouth opening while the remainder may be arranged in one circle of ten or as an intermediate circle of six and an outer circle of four. In all the definitely *Euchromadora* species usually the outer sense organs only are in the form of setae while in the others the intermediate circle is also composed of setae.

THE STRUCTURE OF THE CUTICLE

The structure of the cuticle will be considered in detail later but it is only fair to stress at this point that its analysis is very difficult. However the following features are common to all those species with complex cuticles. The cuticle, except the extreme anterior end, is dark in colour, thick and marked by large, elongate punctations anteriorly, at least. In addition, in many forms, the components of the cuticle appear to move when the focus is adjusted under very high magnifications. This elaborate structure is best understood against the functional background imposed by the design of the nematode body but I would point out that I have never been able to find any indication of fine "lines" connecting the punctations in a network or any other arrangement.

The long, thin cylindrical nematode body with its system of longitudinal muscles operating against an internal hydrostatic pressure produces two inevitable and conflicting mechanical requirements: longitudinal flexibility combined with radial or tangential strength (Inglis, 1964). This has been overcome during the evolution of various groups of nematodes in one of, or a combination of both of, two ways: by the evolution of either a system of cross spiral, helically arranged fibres or a series of transverse rings of dense material within the cuticle.

The spiral fibre method resolves both problems at the same time but the transverse ring method introduces further problems, particularly a loss of flexibility and the presence of regions of relative weakness in the cuticle between the strong, dense rings of sclerotized material. The latter problem has been resolved in a number of ways such as the development of overlapping flaps of dense material which lie over the weaker, less dense inter-annular material or by the development of tiling (de Coninck, 1942). The most complicated method, however, appears to be that evolved in some of the Chromadoridae, particularly those referred to the genus *Euchromadora*,

in which the inter-annular regions are strengthened by processes bridging the gaps between the annules like the teeth of a comb.

In the typical *Euchromadora* species, in which the dorsal onchium is massive and solid and the oesopharhabdion bears series of small denticles, the cuticle always has non-punctate regions running down the dorsal and ventral surfaces of the body (see Coles, 1965, Fig. 1 and discussion) while in the hollow onchium forms, in which there are flanges laterally in the oesophastome, the cuticle does not have clear strips dorsally and ventrally. Instead elongate punctations occur over the whole surface of the body along its whole length, except on four regions, dorso- and ventro-lateral in position, where the punctations are replaced by prominent articulating plates (see Text-fig. 68 and also Steiner & Hoeppli, 1926, Pl. 1, 2, figs. 1, 3, 4, 5).

The non-punctate region of the cuticle at the anterior end of the body is shallow and, as a corollary, the amphids tend to lie near the anterior end in *Euchromadora* species, while in the other group of species this non-punctate region is relatively extensive and the amphids lie relatively far posteriorly. The amphids themselves differ in being rather indistinct in *Euchromadora*, where they are bordered by slightly raised fringes of cuticle, while in the other forms they are distinct with very prominent wide cuticular fringes round their edges.

In all the descriptions of the cuticle that follow it must be remembered that the conditions are reversed roughly half way along the length of the body. Thus when anteriorly directed processes are described as occurring within the cuticle on the anterior end of the body, those on the posterior half of the body will be directed posteriorly.

Finally in all the descriptions of the cuticle the modifications referred to are represented by a dense, dark component lying within the cuticle and embedded in a less distinct matrix. This dense component is generally in the form of transverse annules which, in longitudinal section, are roughly rectangular with the short side of the rectangle lying parallel to the antero-posterior axis of the body. (Text-figs. 60, 67, 69.)

EUCHROMADORA de Man, 1886

It is usual to defer using new names for taxa until the evidence on which the taxa are based has been presented. Here there are so many changes in nomenclature and so much discussion of evidence that to do so would make the entire presentation even more complicated than it already is, or will become. I shall, therefore, present the argument and evidence under various headings, usually the name of the genus I finish by delimiting.

The genus which is central to the morphological argument is *Euchromadora* which I consider first.

Head Structure

The immediate result of the detailed study of the structure of the head and oesophastome is to suggest that it is of little value in delimiting species within the genus. One difficulty is the technical problem imposed by the small size of some of the specimens and another is that the appearance of the dentition varies dependent

upon the degree to which the mouth is open or closed. The following features are, however, common to all the specimens, of all the species studied.

There is always a row of denticles along the dorsal edge of the oesopharhabdion anterior to the large, solid dorsal onchium which is usually obviously bent about its mid-length. The anterior edge of the oesophastome is always developed as an anteriorly directed process on the most dorsal edge of the lateral wall of the oesophastome, and sometimes a similar development appears to be present on the lateral edges of the dorsal wall also.

The lateral and ventral walls of the oesophastome are always distinct and the lateral bear at least four rows of transversely arranged small solid cuticular denticles of which the most posterior (i.e. those lying deepest or most posterior within the oesophastome), Row-IV, tend to be largest and generally arise from a common thickened cuticular base or ridge. In some species the distribution of the denticles on the lateral walls appears to be characteristic but it is impossible to be sure as yet. Nevertheless there is almost invariably what looks like a swollen pad bearing two fairly prominent denticles with, frequently, a few smaller denticles between them, on the extreme anterior limit of the lateral wall (Row-I) with, posterior to this level, a further two rows, Rows II and III, anterior to the most posterior Row-IV.

The distribution of the denticles on the ventral walls of the oesophastome appears to be a little more valuable in delimiting species but here also some uncertainty remains. The anterior limit of each of the ventral walls is frequently obvious in *en face* views as a distinct curved rod-like ridge. This is followed more deeply, or posteriorly, by a number of small solid denticles with, at the extreme posterior depth of the oesophastome, a number (usually three) of large solid tooth-like structures which arise, typically, from a massive plate (Text-figs. 9, 10).

In detail the dentition in the various species I have studied is as follows.

Euchromadora vulgaris (Text-figs. 1-5).

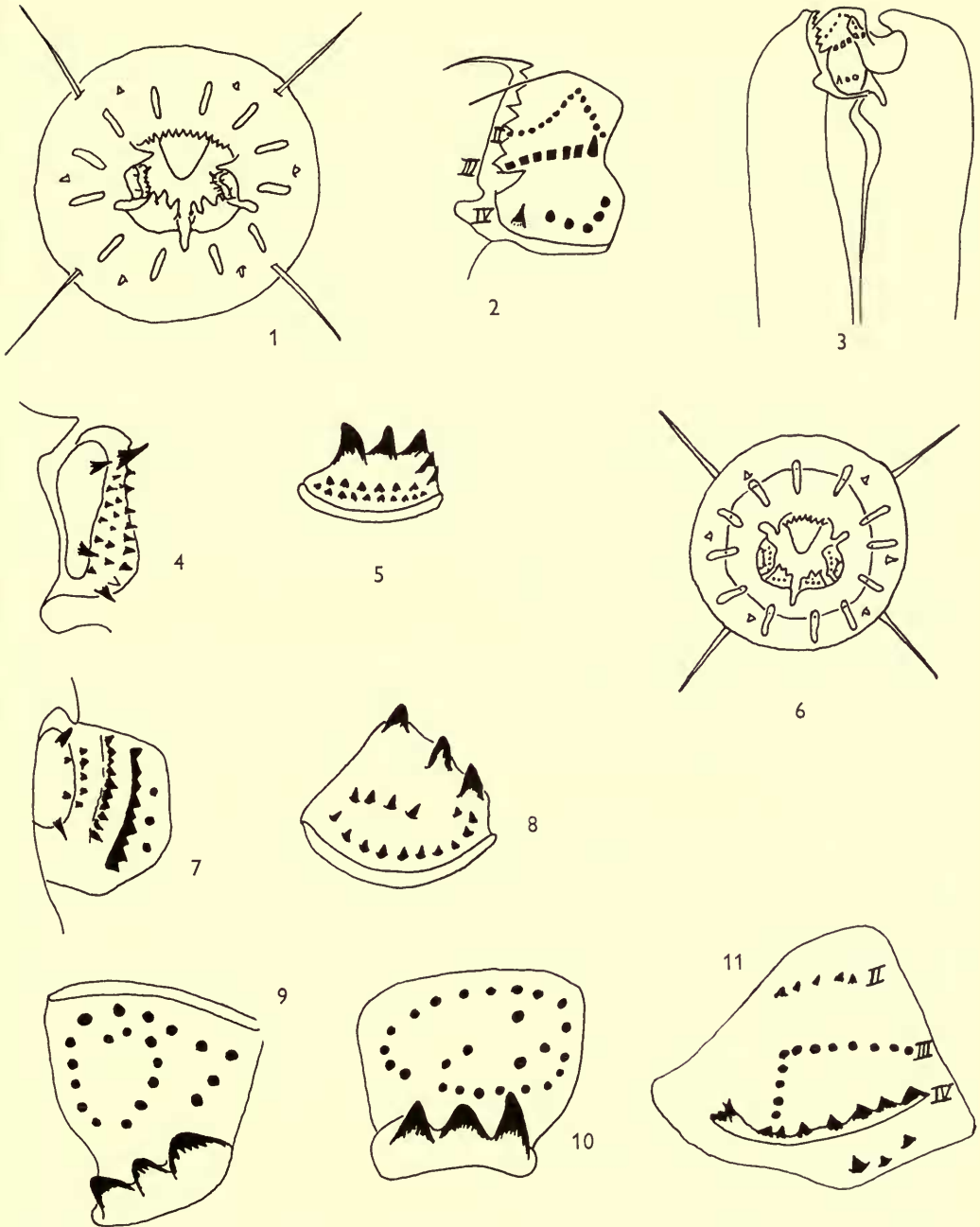
Lateral walls. Row-I: two large denticles, no smaller ones seen; Row-II: denticles small, row bent anteriorly (Text-fig. 2); Row-III: straight and prominent with most dorsal denticles larger than others; Row-IV: denticles prominent, row slightly L-shaped, largest most ventral (Text-figs. 2, 4).

Ventral walls. There are two rows of small denticles near the anterior edge, three very prominent and massive denticles posteriorly (i.e. deep within oesophastome) which arise from a distinct plate and one or two prominent denticles on the edge of the wall where it meets the ventral extension of the lumen. These denticles vary in appearance, possibly because of different angles of examination.

This description, based on light microscope studies, has been confirmed by electron scan (Stereoscan) examination.

Figs 1-11—*contd.*

gaulica. 6. *En face* view of head. 7. Lateral oesophastomal dentition, *en face* (sketch), dorsal towards top. 8. Left ventral dentition of oesophastome *en face* (sketch). 9-10. Inner views of ventral walls of oesophastome on one specimen. Ventral extension of oesophastomal lumen lies between figures. 11. Lateral dentition of oesophastome viewed from inner surface, dorsal to left.



FIGS. 1-11. 1-5. *Euchromadora vulgaris*. 1. *En face* view of head. 2. Oesophastomal dentition (sketch, detail). 3. Lateral view of anterior end of oesophagus, dorsal to right. 4. Lateral dentition of oesophastome *en face* (sketch), dorsal towards top. 5. Left ventral dentition of oesophastome *en face* (sketch). 6-11. *Euchromadora*

Euchromadora gaulica (Text-figs. 6-11).

Lateral walls. Row-I: tiny denticles between large dorsal and ventral denticles; Row-II: short, straight with tiny denticles; Row-III: L-shaped with short leg directed posteriorly and long leg transversely; Row-IV: very prominent with denticles arising from a distinct, curved, basal flange. In addition there are a number (three seen) of thorn-like denticles arising from the most posterior level of the wall. I am not absolutely certain but these latter structures appear to be additional to the more usual four rows of denticles. (Note that in Text-fig. 11 the ventral surface of the body is towards the right and the drawing shows the inner surface of the wall.)

Ventral walls. The small anterior denticles are arranged in a crude spiral (Text-figs. 8, 9, 10) while there are three massive, basal onchia arising from a very prominent plate. Three illustrations of the conditions are given of which Text-fig. 8 is taken fully *en face*, while Text-figs. 9 and 10 show the two ventral walls of one specimen. In this latter case the walls are viewed from the inner surface and are taken from a wholly dissected specimen. Text-fig. 9 shows the left wall and Text-fig. 10 the right. It should be noted that the spiral of denticles occurs towards the lateral surface of the body. In other words the right-hand side of Text-fig. 8 corresponds to the median ventral extension of the lumen while the left-hand side is contiguous with the lateral wall of the oesophastome.

Euchromadora striata (Text-figs. 12-24).

Lateral walls. Row-I: usual two prominent denticles with series of smaller denticles between them; Row-II: curves anteriorly and all denticles are about same size; Row-III: very slightly bowed anteriorly, denticles all about same size; Row-IV: denticles relatively massive, few in number and arising from very prominent basal plate.

Ventral walls. The occurrence of some variation could be established possibly because of the relatively large size of specimens of this species. The small, anterior denticles lie in three rows of which those of the most anterior row are consistently smaller than those of the others. In addition a varying number of tiny denticles can occur (or be seen) in some specimens but these are always restricted to the more lateral region of the wall (Text-figs. 14, 20). There are two, sometimes three, large denticles deep on the ventral wall of which two are consistently present near the edge of the ventral lumen (Text-figs. 15, 20). This may vary because of the contraction of the mouth opening so that in some specimens the large denticles are not quite on the edge (Text-figs. 14, 16). The large posterior onchia are very obvious in lateral view (Text-figs. 19, 24).

Euchromadora eileenae (Text-figs. 31-37).

The dentition of the oesophastome in this species is very similar to that in *E. gaulica*.

Lateral walls. All rows of denticles slope posteriorly from dorsal side (Text-fig. 34). Row-I: two prominent denticles only; Row-II: relatively few, small denticles in an almost straight line; Row-III: rather short and slightly bowed anteriorly; Row-IV:

straight, denticles prominent of which most dorsal is larger than the remainder, all arise from a definite plate, at least in one specimen studied *en face* (Text-fig. 37). Posterior to Row-IV are two, sometimes three, prominent dorsal edge of the walls.

Ventral walls. The denticles form a definite curved or spiral arrangement with the spiral towards the lateral surface of the body. Towards the mid-ventral extension of the lumen there are two large denticles but there does not appear to be any definite plate associated with them (Text-fig. 36) nor are they always present, or at least have not always been seen (Text-fig. 35).

Cuticle Structure

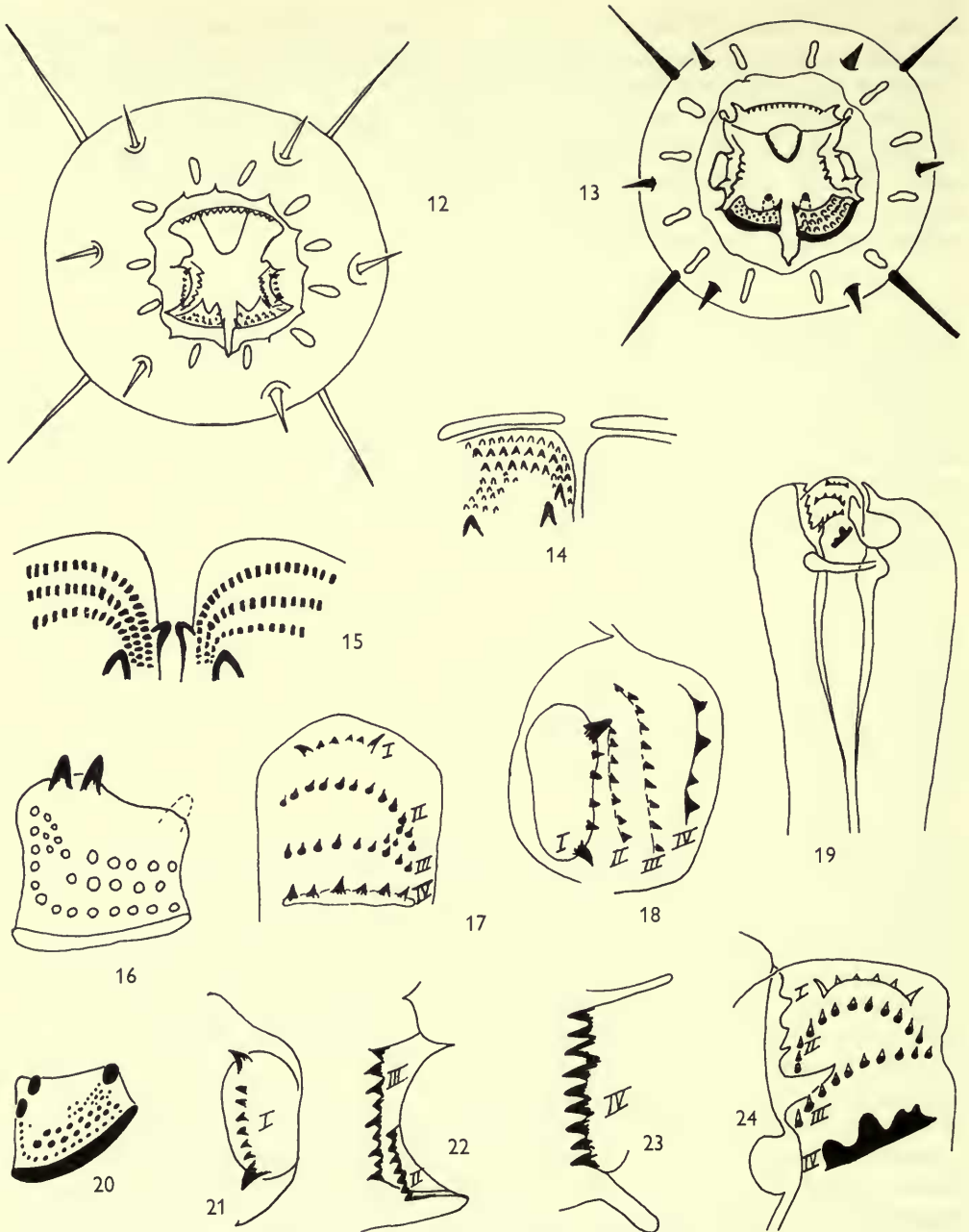
The detailed structure of the massively punctate cuticle occurring over the anterior region of the body in *Euchromadora* has been described elsewhere (Inglis, 1964) but, because at that time I was only considering the modifications of the punctation system, the structure of the unpunctate cuticle was not discussed nor were the lateral plates considered. Briefly, the cuticle consists of a series of annules of dense material embedded in a general covering of less dense material and all the structure usually described as cuticular modification or simply as cuticular structures are represented by these dense components.

Each annule is represented on the surface of the cuticle by a transverse striation and the annules themselves can be extremely complicated. At the anterior end of the body each annule can be thought of as composed of three subsidiary annules which together form a somewhat rectangular block in longitudinal section (Text-fig. 60). The outermost sub-annule is developed anteriorly as a thin, wedge-shaped flange which lies over the posterior edge of the next most anterior annule and posteriorly is curved to form a region covered by the flange from the anterior edge of the next most posterior annule.

The innermost sub-annule is more regularly rectangular in longitudinal section but from about the middle of the oesophagus length posteriorly it bears a lateral peg or plate which projects anteriorly to lie under the next annule anteriorly. There is a slight concavity on the posterior edge of this innermost sub-annule, immediately posterior to the anteriorly directed peg, into which the anteriorly directed peg from the next more posterior annule fits. These pegs I have called "lateral plates" and it should be noted that they lie within the lateral chords of the hypodermis and are below the lateral rod-like punctations when the cuticle is viewed from the surface (Text-figs. 60-61).

In some specimens the lateral plates appear to be represented by a series of granules of dense material but it is uncertain whether or not this is due to studying pegs in optical section as I have not had sufficient specimens to warrant treating them with sodium hypochlorite. It may be noted in passing that this is not the system to which Steiner (1918) refers, as he is dealing with the true punctation rods which lie above the lateral plates and that Wieser & Hopper (1967) appear to have confused the two sets of structures in their discussion of *Euchromadora gaulica*.

The massive punctation blocks arise from the region between the outermost and innermost sub-annules and can be pictured as a third sub-annule. These blocks which are circular in transverse section project anteriorly on the anterior half of the



FIGS. 12-24. *Euchromadora striata*. 12. *En face* view of head. 13. *En face* view of head of another specimen. 14. Dorsal-oblique view of inner surface of ventral oesophastomal walls (sketch). 15. As fig. 14, but extremely regular condition with only two large onchia (sketch). 16. Right ventral wall of oesophastome *en face* (sketch). 17. Inner surface of lateral wall of oesophastome, dorsal to left (sketch). 18. Right ventral, wall of oesophastome *en face* (sketch), dorsal towards top. 19. Lateral view of

body to lie between the similar blocks developed on the next most anterior annule. The blocks are further connected to both the outermost sub-annule and the innermost over their posterior halves as I have illustrated elsewhere (Inglis, 1964, Figs. 13, 15). The conditions described above apply to the anterior half of the body. Over the posterior half the conditions are reversed so that the outer sub-annules are extended posteriorly instead of anteriorly and the punctation blocks and lateral plates are also directed posteriorly instead of anteriorly.

To revert to the anterior cuticle, the large punctations disappear over two strips both dorsally and ventrally so that a V-shaped strip of punctations projects posteriorly along the dorsal and ventral surfaces of the body (see Coles (1965) particularly Fig. 1), until by about the posterior end of the oesophagus the dorsal and ventral cuticle is marked only by transverse striations. Meanwhile the large elongate punctations become slimmer and longer and are restricted to a fairly narrow zone running down the lateral surfaces of the body (Text-figs. 60-63).

The structure of the cuticle in *Euchromadora vulgaris* has been studied by light and electron microscopy by Watson (1965) but most of what she reports is based on an examination of the dorsal or ventral region of non-punctate cuticle. This explains the apparent discrepancy referred to by Lee (1966). In particular Watson describes the middle layer in this non-punctate region as consisting of overlapping plates, with which I agree, but it is the origins of these plate-like structures (a description which only applies to the view in longitudinal section) which is particularly interesting.

The lateral surface cuticle is relatively thick and is marked by the obvious punctations which correspond to the layer of rods sandwiched between the two other layers like teeth of a comb (Text-figs. 60, 65). Dorsally and ventrally the cuticle, which lacks such punctations, is much thinner. Each annule, in longitudinal section, is a thin wedge-shape with the thinner edge outermost and overlying the next more anterior or posterior annule (Text-fig. 63). The region of transition between these two zones of modification is most interesting since it explains, among other things, some of the features of the cuticle described and illustrated by de Man (1886). Before describing this transition zone I should stress that I have only been able to confirm this detail in *E. vulgaris*, *E. gaulica* and *E. loricata*.

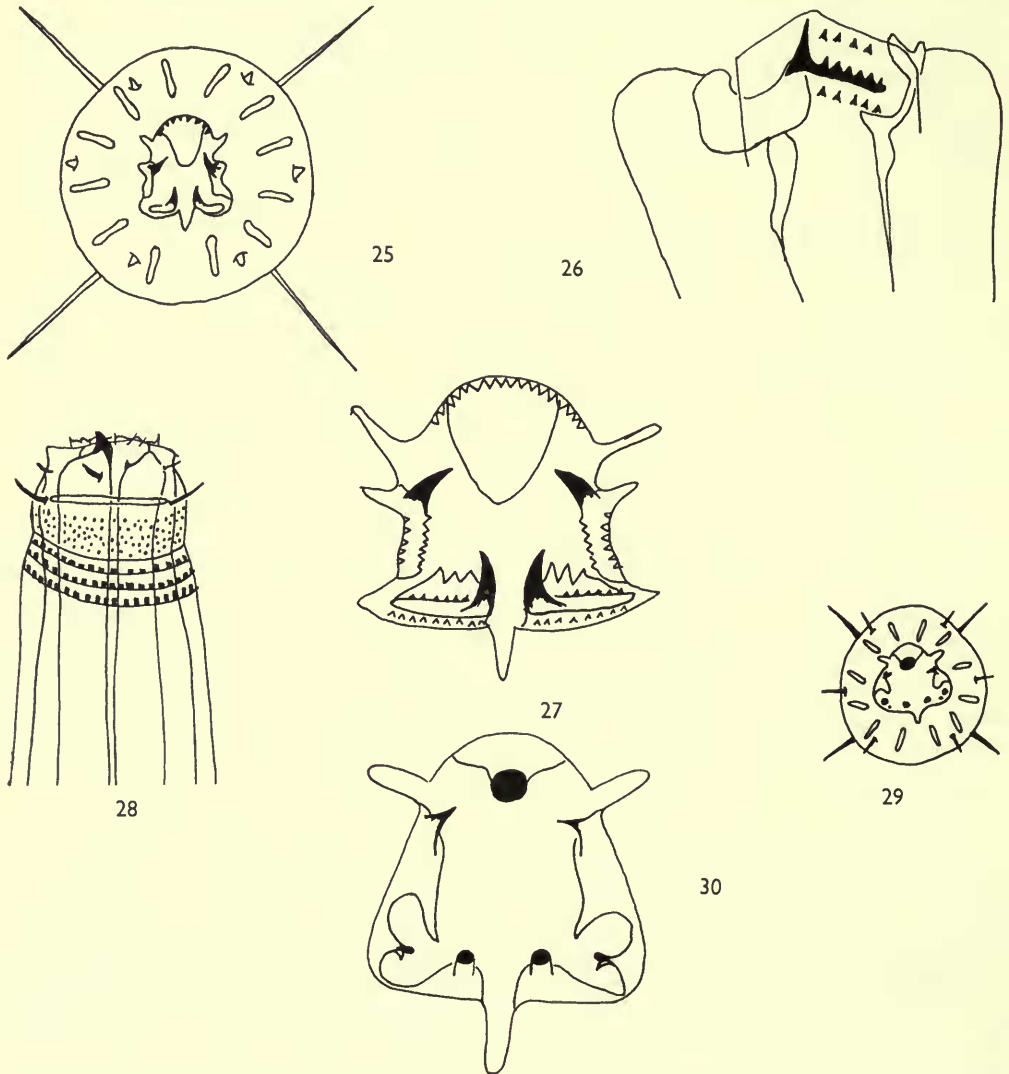
The change from the lateral region with long punctations to the dorsal and ventral region without such punctations occurs very sharply and involves (on the anterior end of the body) the displacement of the innermost sub-annule of the dense component of the cuticle posteriorly relative to the remainder of the annule. At about the same level the punctation sub-annule becomes solid and it also is displaced posteriorly, but not to the same extent as the innermost. The combination of these displacements is to produce a wide, thin wedge-shaped (in section) annule, so that although the annules only overlap each other slightly on the lateral surface of the cuticle

Figs. 12-24—*contd.*

anterior end of oesophagus, dorsal to right. 20. Right ventral wall of oesophastome *en face* (sketch). 21-23. *En face* optical sections through lateral wall of oesophastome, dorsal towards top (sketches). 21. Denticles of Row-I. 22. Denticles of Rows-II and III. 23. Denticles of Row-IV. 24. Lateral wall of oesophastome viewed from outer surface (sketch), dorsal to right.

the overlap is considerable on the dorsal and ventral surfaces (Text-figs. 60-64).

As a consequence each annule of dense material when considered alone is not a simple ring but is a narrow thick sector with punctation processes laterally and a thin, wide, wedged sector dorsally and ventrally. This is illustrated in a very simplified way in Text-fig. 65. One consequence of this relative displacement of the



FIGS. 25-30. 25-27. *Steineridora lovicata*. 25. *En face* view of head. 26. Lateral wall of oesophastome viewed from outer surface (sketch), dorsal to left. 27. *En face* detail of dentition of oesophastome (sketch). 28-30. *Graphonema georgei*. 28. Lateral view of anterior end of body. 29. *En face* view of head. 30. Oesophastomal dentition *en face* (sketch) dorsal towards top.

constituent sub-annules is that the analysis of the modification in whole mounts is very difficult because one edge of one sub-annule moves posteriorly relative to the others while the others, which can still be recognized in the specimen, remain at the same level. Over the whole diameter of the body the anterior edge of each annule remains at the same transverse level and appears as a straight striation running round the body. The general appearance of this cuticle is shown in Text-fig. 64, but it should be remembered that this illustration is taken from a much compressed specimen.

There are still some minor discrepancies between this description and that given by Watson (1965), particularly the condition shown in her Fig. 3A in which are illustrated what she interprets as the "rod-like bodies" of de Man. However I suspect that what is shown is the anterior region just posterior to the amphids in which the cuticle is supported by rod-like punctations. This interpretation is supported by the fact that the cuticle shown in Fig. 3A is obviously considerably thinner than that shown in Watson: Fig. 1A which in turn is, I already know, considerably thinner than that in which the typical, massive punctation blocks or processes occur.

To complicate matters even further I suspect that the illustrations of the overlapping plate-like cuticle were taken from the transition zones at the anterior end of the body so that there are structures present which are definitely not present more posteriorly. I have, in fact, seen structures by the light microscope which resemble the transverse rings of dense material in Layer 1 in Watson's Fig. 2 but they cannot be analysed in my material. This feature deserves further study. Finally it is perhaps worth pointing out that the direct attachment of the muscles to the cuticle described by Watson is the feature responsible for the description of the basal layer by several other workers as longitudinally striated or with longitudinal fibres.

In view of these observations the genus may be rediagnosed thus:

EUCHROMADORA de Man, 1886

Chromadoridae: Cuticle: complex with large, prominent, elongate hexagonal or ovoid punctations anteriorly and posteriorly which correspond to processes developed within cuticle from one side of each annule only; similar, but slimmer markings restricted to lateral surface over middle length of body; no punctations on dorsal or ventral surfaces over middle length of body; "lateral plates" generally well developed; no lateral differentiation.

HEAD: large, solid dorsal onchium preceded by denticles on anterior dorsal edge of oesophastome; transverse rows of small, solid denticles on lateral walls of oesophastome; similar denticles anteriorly on ventral walls of oesophastome with, frequently, larger denticles posteriorly arising from a distinct plate; cephalic sense organs in three circles of which the outer is composed of four setae; mouth surrounded by twelve rugae; amphids elongate transverse slits without marked fringes of cuticle surrounding them; oesophagus without definite posterior bulb.

MALE: gubernaculum with prominent, generally hammer-shaped or L-shaped lateral pieces; no pre-cloacal supplements or other modifications of cuticle; tail relatively short and stout.

TYPE SPECIES: *Chromadora vulgaris* Bastian, 1865. Described above in part and reference confirmed by de Man's (1886) and Coles' (1965) descriptions in addition to the study of specimens.

OTHER SPECIES. The following species may be definitely referred to the genus *Euchromadora* as restricted by this diagnosis because they possess or appear to possess this combination of characters.

E. gaulica Inglis, 1962. Redescribed above in part. The gubernaculum has been re-examined in European specimens and the presence of the two minute denticles near the posterior end which are figured and described by Wieser and Hopper (1967) has been confirmed.

E. striata (Eberth, 1863). Redescribed below, page 191.

E. meadi Wieser & Hopper, 1967. Retained on the basis of the original description.

E. permutabilis Wieser, 1954. Retained on the basis of the original description.

E. tokiokai Wieser, 1955. Retained on the basis of the original description.

E. eileenae sp. nov. Described below, page 193.

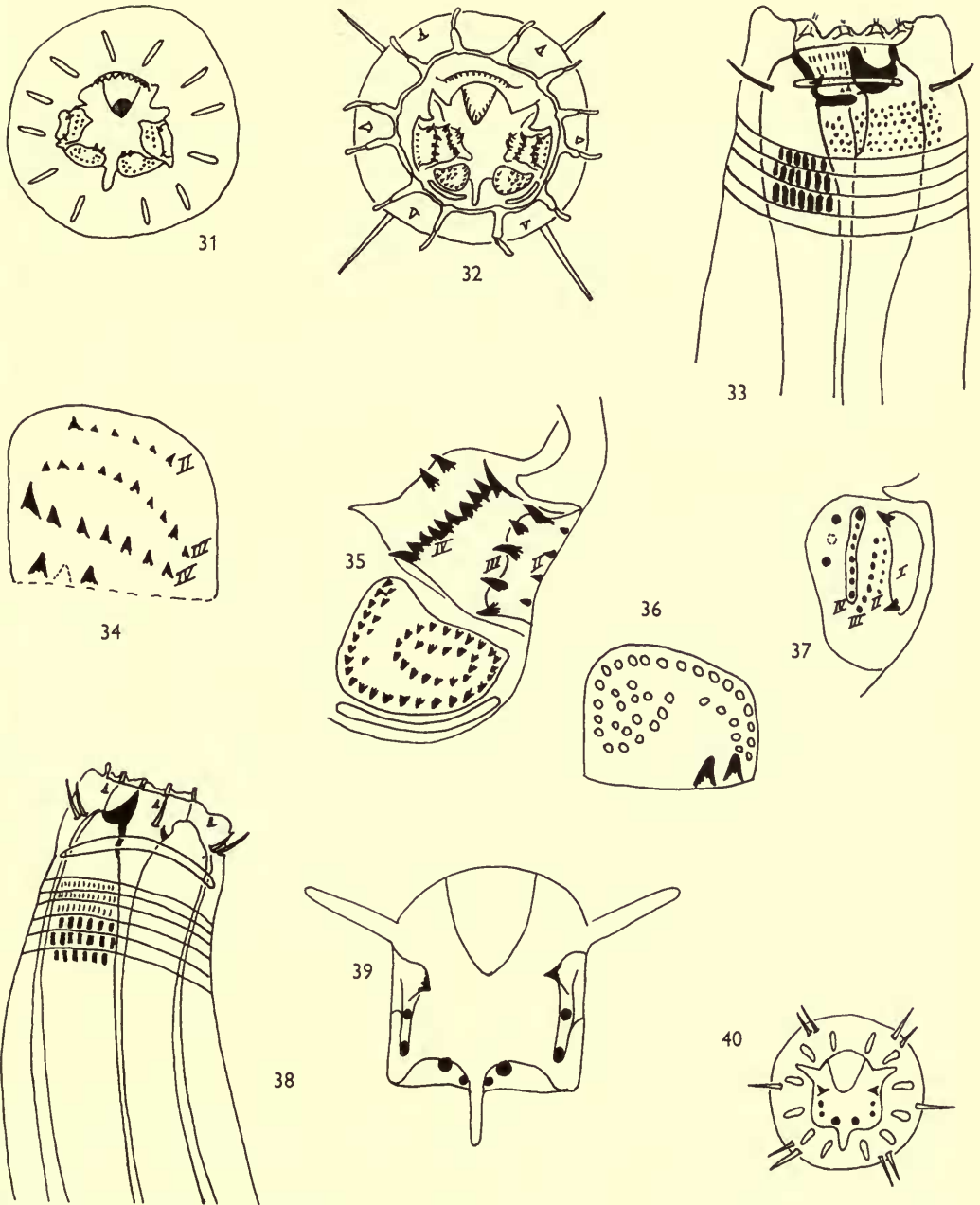
The disposition of other species usually referred to *Euchromadora* is listed on page 201.

STEINERIDORA gen. nov.

This new genus is proposed for some of those species which are generally referred to the genus *Euchromadora* but which differ most obviously from the species discussed above in possessing a distinct posterior oesophageal bulb. In this group are seven nominal species: *E. archaica* Steiner & Hoeppli, 1926; *E. amokurae* (Ditlevsen, 1921) (although Ditlevsen points out that his illustration tends to exaggerate the oesophageal bulb); *E. loricata* (Steiner, 1916); *E. adriatica* (von Daday, 1901); *E. dubia* Steiner, 1918; *E. denticulata* Cobb, 1914 and *E. stateni* Allgén, 1930.

E. loricata, of which I have studied specimens in detail, differs from the typical non-bulbed *Euchromadora* species in several other morphological features, many of which were reported by Steiner and Hoeppli in 1926 in describing *E. archaica*. The punctations in the cuticle, which are processes exactly as in *Euchromadora*, remain much the same size over the whole length of the body in contradistinction to the condition in *Euchromadora* (s.s.) where they become markedly thinner and longer over the middle length of the body. This is, I think, what Steiner and Hoeppli mean when they describe the cuticle of *E. archaica* as ". . . rather undifferentiated structure compared with other species; . . ." (Steiner & Hoeppli, 1926, page 571). There are clear non-punctate regions running down the dorsal and ventral surfaces of the body.

The structure of the oesophastome is recognizably *Euchromadora*-like but, although the typical dorsal onchium is present preceded by a row of denticles along the anterior dorsal edge of the oesophastome, it is a characteristic square shape (Text-figs. 25-27). The dentition of the lateral and ventral walls of the oesophastome is also similar to that of *Euchromadora* species with at least three transverse rows of small denticles on the lateral walls (Text-fig. 26). However the lateral walls also bear very prominent, sickle-like dorsally directed cuticular onchia which arise from distinct



FIGS. 31-40. 31-37. *Euchromadora eileenae*. 31. En face view of head. 32. En face view of head from another specimen. 33. Lateral view of head. 34. Lateral dentition of oesophastome viewed from inner surface (sketch), dorsal to left. 35. Oesophastomal dentition en face (sketch) from specimen with mouth wide open, shown in fig. 32. 36. Inner surface of left ventral wall of specimen shown in fig. 31 (sketch). Note presence of large paired denticles and spiral arrangement of small denticles. 37. Lateral dentition of specimen illustrated in fig. 31 en face (sketch). 38-40. *Austranema alii*. 38. Anterior end of body. 39. Dentition of oesophastome en face (sketch). 40. En face view of head.

ridges, the edges of which bear very tiny onchia (Text-figs. 26, 27). This ridge, and associated minute denticles, represents the middle of the three lateral rows of denticles.

Ventrally a similar pair of sickle-like onchia occur near the ventral edges of the ventral walls and these also arise from distinct transverse blade-like ridges which bear minute denticles along their anterior edges (Text-fig. 27). In addition on the ventral walls there is, possibly, a row of very tiny denticles anterior to the basal flanges of the large onchia while there is a set of three large onchia fairly deep in the oesophastome which arise from a plate-like base, exactly as in some of the *Euchromadora* species.

The same dentition is illustrated and described by Steiner and Hoeppli (1926) for *E. archaica* and I have established that the same conditions occur in *E. adriatica*, so far as is possible in whole mounts from the lateral aspect.

I therefore propose to refer these species to a distinct genus:

STEINERIDORA gen. nov.

Chromadoridae: Cuticle: complex with relatively stout, elongate punctations anteriorly and posteriorly which correspond to processes developed within the cuticle from one side of each annule only; similar and equally large, punctations continue on lateral surfaces of cuticle only over the middle region of body; no punctations on dorsal and ventral surfaces over much of middle body length where each annule is wider than it is laterally; "lateral plates" poorly developed; no lateral differentiation.

HEAD: large, squarish, solid dorsal onchium; denticles on anterior, dorsal edge of oesophastome; rows of small denticles on both ventral and lateral walls of oesophastome and large, curved, horn-like onchia projecting into oesophastome; cephalic sense organs in three circles of which outer is composed for four setae; mouth surrounded by twelve rugae; amphids elongate, transverse slits, not bounded by prominent fringe of cuticle; oesophagus with definite posterior bulb.

MALE: gubernaculum with prominent L-shaped lateral pieces; no pre-cloacal supplements or other modifications of cuticle; tail relatively short and stout.

TYPE SPECIES: *Spilophora loricata* Steiner, 1916.

OTHER SPECIES: *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S. (?) dubia* (Steiner, 1918) *sp. inq.*

The position of the remainder of the seven nominal species with a posterior bulb to the oesophagus is difficult to establish, largely because of the poverty of the original descriptions. However, *Spilophora amokuræ* Ditlevsen, 1921 fairly clearly has a hollow dorsal onchium (Pl. 2, fig. 4 in Ditlevsen, 1921) and has a very extensive unmarked region of cuticle at the anterior end of the body (see further discussion below, page 182); *Euchromadora dubia* Steiner, 1918 is insufficiently described for any certain opinion to be reached but appears to be referable to *Steineridora* although only as a *species inquirendum*; *E. denticulata* Cobb, 1914 is poorly described but because it appears to have a hollow or hollow-type dorsal onchium and the intermediate circle of cephalic sense organs is setose it is not referable to either

Euchromadora or *Steineridora* (see below, page 188); *E. stateni* Allgén, 1930 is treated as a synonym of *E. denticulata* by Wieser (1954) but is better treated as a *species dubia* as suggested by Coles (1965). Nevertheless it should be noted that the illustration of the head shows that *E. stateni* is not referable to *Steineridora* nor to *Euchromadora* since it has a hollow-type anteriorly directed dorsal onchium, an intermediate circle of six setae and an extensive non-punctate region at the anterior end of the body.

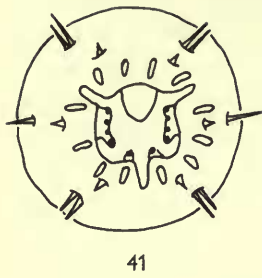
PARAPINNANEMA gen. nov.

In a new species from Western Australia, which is later named *Parapinnanema wilsoni*, the cuticle is thin and marked by a series of fine annules, in which there are fine elongate punctations, for about one head diameter posterior to the anterior end of the body. Posterior to this level the cuticle thickens very rapidly and is very prominently marked by obvious "battlement-like" punctations (Text-figs. 66, 97). The cuticle becomes thinner, rather slowly, over the posterior quarter of the length of the oesophagus and the markings become smaller and less pronounced but are still obviously battlement-like. Such a region of thick cuticle is a characteristic feature of most of the species in which the cuticle is battlement-like, although never as strongly as in *P. wilsoni* where it is one of the most startlingly obvious features of the species even under a low-power stereoscopic microscope (Text-fig. 97).

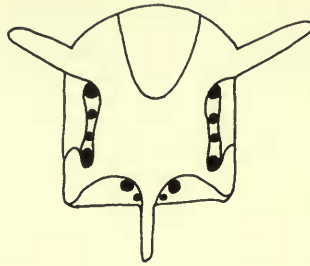
It should be noted that it is possible to get the impression that the cuticle is modified by a series of rods and dots over some areas but this depends upon the focusing and the extent to which the specimen being studied is under pressure. An additional complication in interpreting the structure of the cuticle from whole specimens is that, as in *Euchromadora*, each annule of the dense component of the cuticle consists of three or two sub-annules which are generally skewed so that one never lies immediately above another. As a result it is easy to interpret the conditions as representing two inner annules to each outer annule. This never appears to be true when the annules are separated by using sodium hypochlorite.

The punctation markings occur over the whole surface of the body, both dorsally and ventrally as well as laterally and the battlement-like markings become more pronounced again over the region just anterior to the cloacal opening or the anus and continue like this over the tail. The annulation is wide and the transverse striations on the surface of the cuticle are deep and pronounced (Text-figs. 73-75).

In detail the cuticle resembles *Euchromadora* in that each annule consists of two, or three (depending on interpretation) sub-annules of which the outermost is curved anteriorly (on the anterior half of the body) to form a strip overlying the posterior edge of the next immediately anterior annule. The innermost is similar to that in *Euchromadora*, consisting of a solid sub-annule which is slightly rounded along both the anterior and posterior edges. The major difference between the *Euchromadora* and *Parapinnanema* cuticles is that in the latter there are processes developed on both sides of the annules, on the middle of the body-length, about the middle of the thickness of the cuticle (Text-fig. 72), instead of on only one side as in *Euchromadora*, and there do not appear to be clear channels passing completely through the middle sub-annule.



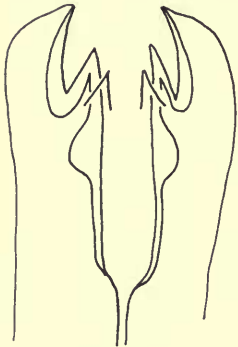
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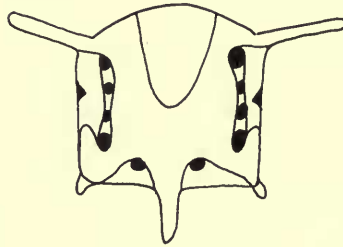
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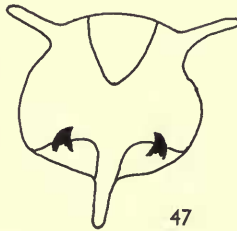
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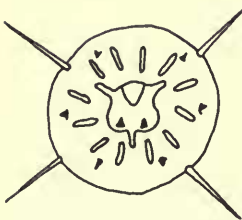
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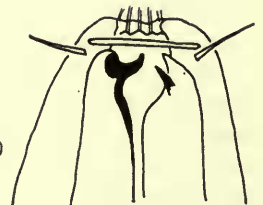
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FIGS. 41-50. 41-43. *Austranema colesi*. 41. *En face* view of head. 42. Oesophastomal dentition *en face* (sketch). 43. Lateral view of anterior end of oesophagus, dorsal to right. 44-46. *Austranema shirleyae*. 44. Ventral view of oesophastome showing ventral onchia and lateral flanges in optical section (sketch). 45. Oesophastomal dentition *en face* (sketch). 46. Lateral view of anterior end of oesophagus, dorsal to right. 47-50. *Protochromadora scampae*. 47. Oesophastomal dentition *en face* (sketch) 48. Detail of dorsal onchium (sketch) 49. *En face* view of head. 50. Lateral view of anterior end of body.

This modification is apparent in a different way in the thick cuticle at the anterior end of the body where the battlement-like markings are very obvious. Here when the cuticle begins to become very thick the anterior edge of the outer annule becomes notched so that it looks like battlements. Along the posterior edge of the annule posteriorly directed peg-like processes are present which arise from the middle level of the annule (Text-fig. 67). In other words the annules are articulated together by a system derived from both the anterior and the posterior edges (see also Fig. 50b in Filipjev, 1918 and Fig. 52c).

As the cuticle becomes thinner posteriorly the dorso- and ventro-lateral articulating plates (see below) appear about halfway along the length of the oesophagus and the pegs on the posterior edges of the annules move relatively nearer the surface of the cuticle until the modification is restricted to the outer surface of the cuticle. Meanwhile, as the middle pegs move outwards a series of grooves develop in the innermost sub-annule of the cuticle so that there are, in surface view, a series of large battlement-like modifications on the outer level and a series of very fine, short, elongate punctations on the innermost level of the cuticle (Text-figs. 68-71).

Posterior to the posterior end of the oesophagus the battlement-like modifications of the outer surface become smaller, and less distinct, until they almost disappear and are indistinct over roughly the middle third of the body length. At the same distance from the anterior end the fine striations of the inner sub-annule move relatively nearer the middle level of the cuticle as a series of anteriorly and posteriorly directed pegs (Text-fig. 72).

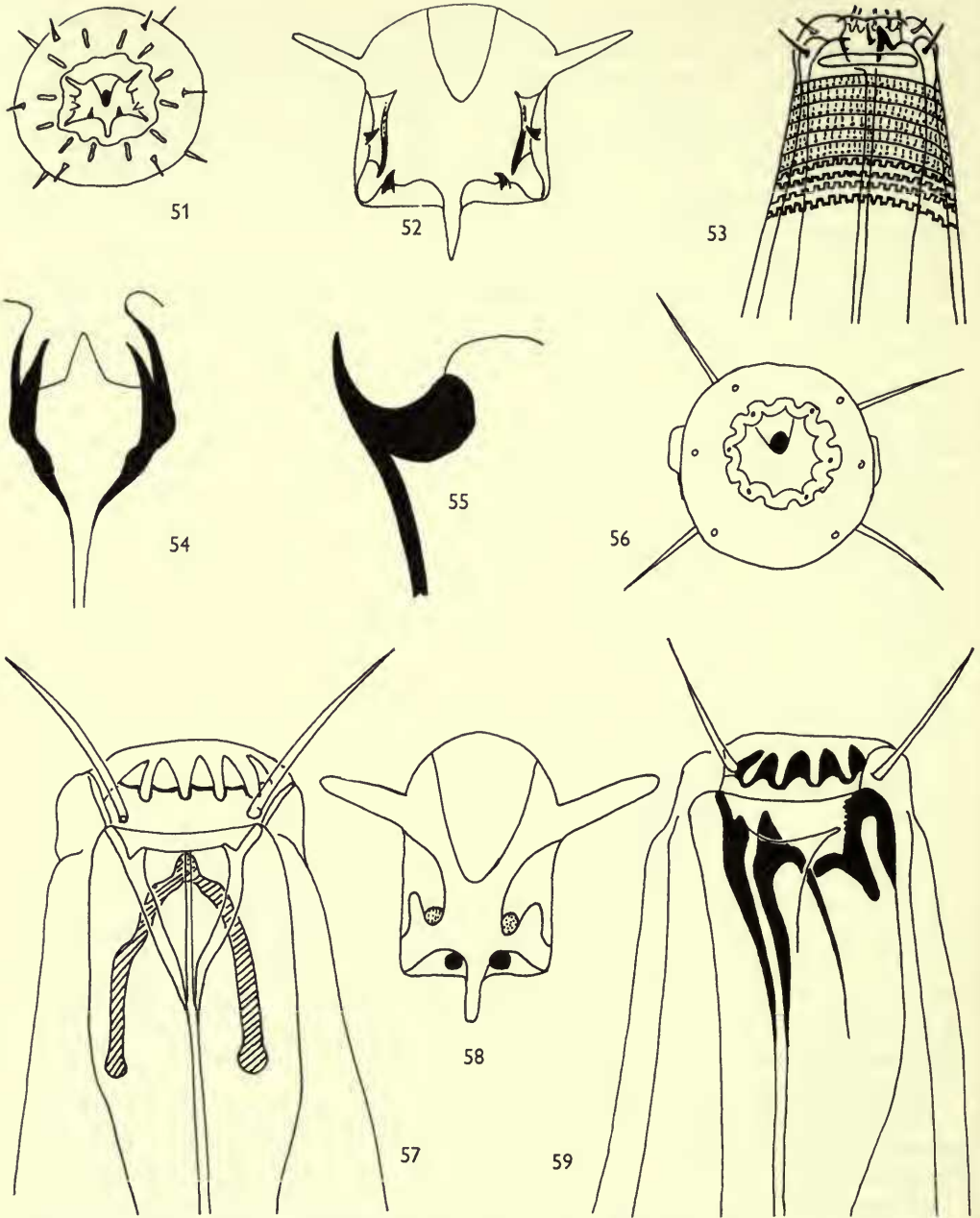
On passing further posteriorly the conditions are reversed; the middle layer of punctation pegs moves inwards to form fine elongate grooves on the inner sub-annules and the battlement-like indentations reappear on the outer surface and those along the *anterior* edge of each annule move inwards, relative to the surface of the cuticle, to form a series of pegs arising from the middle depth of each annule. In other words the conditions are reversed relative to those on the anterior part of the body.

At the level on the length of the body where the punctations are wholly due to the innermost modifications the annules are very skewed (Text-fig. 72) so that on focusing from the surface there appear to be two inner annules to each outer annule, and this condition reverses rather sharply about the middle of the body length. Over this same region of the body there is a distinct straight striation of the surface of the cuticle which runs round the middle of each annule and the annules are delimited anteriorly and posteriorly by wavy lines corresponding to the suppressed battlement-like processes (Text-fig. 75).

Therefore in contrast to the condition in *Euchromadora* there are two systems of punctation rods involved and the annules never widen dorsally and ventrally as in *Euchromadora*.

In addition to all this modification there are interlocking plates along the dorso- and ventro-lateral aspects of the body which are due to the development of interlocking extensions from the *innermost* level of the cuticle and are covered externally by the elongate punctations found on the rest of the cuticle (Text-fig. 68). The cuticle has no clear zones, without punctations, dorsally and ventrally.

The dorsal onchium is hollow (Text-figs. 53, 55) although in some specimens it is



FIGS. 51-59. 51-55. *Parapinnanema wilsoni*. 51. En face view of head. 52. Oesophastomal dentition en face (sketch). 53. Lateral view of head. 54. Dorsal view of oesophastome showing lateral flanges in optical section (sketch). 55. Detail of dorsal onchium (sketch). 56-59. *Hypodontolaimus slacksmithi*. 56. En face view of head. 57. Dorsal view of head. 58. Oesophastomal dentition en face (sketch). 59. Lateral view of head.

difficult to reach a decision. However, in addition to the structure of the cuticle and the form of the dorsal onchium, the specimens are characterized by no denticles along the anterior dorsal edge of the oesophastome, the intermediate circle of cephalic sense organs is setose, there are three circles of sense organs, the lateral walls of the oesophastome bear cuticular flanges which are not divided to form anteriorly directed denticles along their anterior edges so that each flange stands out in *en face* view as a simple, blade-like structure (Text-figs. 51-54). Ventrally there are two anteriorly directed cone-like denticles while in some specimens there appears to be a single denticle on the lateral walls of the oesophastome anterior to the lateral flanges (Text-figs. 51-53).

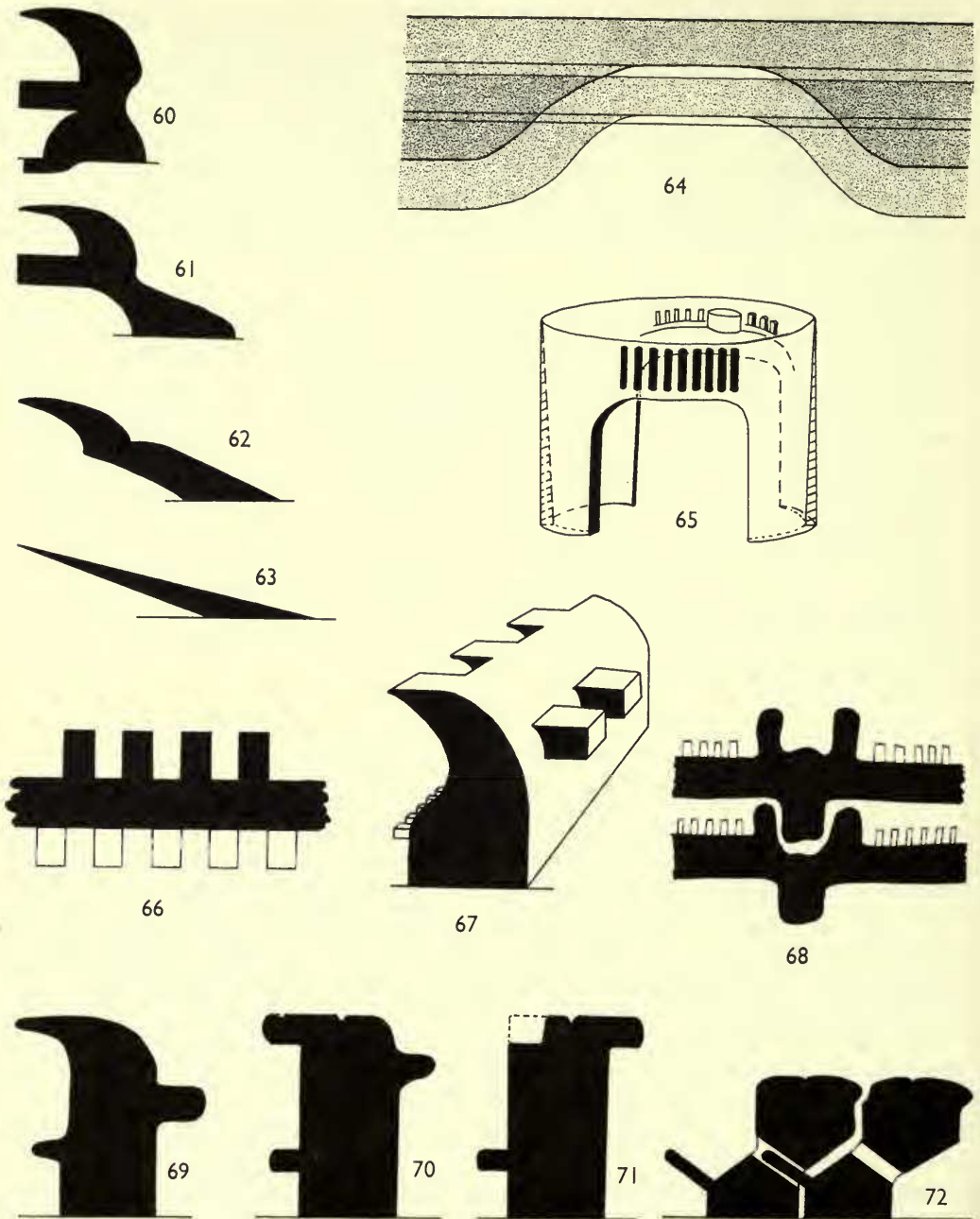
The tail is long and thin, the lateral pieces of the gubernaculum are L-shaped and there is a mid-ventral, thickened, pre-cloacal modification of the cuticle on the males as in *E. colesi* and *N. alii* (see Inglis, 1968 and Murphy, 1965).

The generic name *Odontocricus* Steiner, 1918 is already available for specimens with this massively battlemented type of cuticle. This name was proposed for a new species which was considered sufficiently distinct to warrant reference to a distinct subgenus of *Euchromadora*, *E. (O.) hupferi* Steiner, 1918. The remarkably obvious battlement-like structure of the cuticle is illustrated by Steiner (1918 : Fig. 4) but the species description is based on a juvenile female specimen and it is uncertain that it could ever be recognized again. Equally it is not possible to forecast the continuing uniqueness of the strongly battlemented cuticle so that rather than use a generic name of which the type species is a *species dubia* I propose to erect a new genus for the Australian specimens:

PARAPINNANEMA gen. nov.

Chromadoridae: CUTICLE: without markings on anterior end until posterior to prominent amphids where a series of rods and dots appear; posterior to this level very prominent battlement-like appearance due to presence of processes within cuticle on both anterior and posterior edges of annulations; posterior to oesophagus, over most of body length, punctations slim and elongate but due to second inner layer, most outer layer now reduced to rather wavy lines on outer surface of cuticle; battlement-like cuticle reappears over posterior end of body from slightly anterior to anus or cloacal opening; annulation of cuticle very pronounced and wide; cuticle very thick over roughly length of oesophagus but region just posterior to head thin; no clear zones dorsally and ventrally and annules same width all round body; four files of articulating plates dorso- and ventrolaterally.

HEAD: slightly set-off by appearance of thin covering cuticle relative to conditions more posteriorly; dorsal onchium hollow; no denticles on anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome, without dentate anterior edges; one, solid, cone-like anteriorly directed onchium on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which intermediate consists of six setae and outer of four setae; mouth surrounded by twelve rugae; amphids prominent transverse elongate slits bordered by prominent fringes of cuticle; oesophagus without prominent posterior bulb.



FIGS. 60-72. Structure of cuticle. 60-65. *Euchromadora vulgaris*. 60-63. Successive longitudinal sections through one annule from wholly laterally to wholly ventrally or dorsally showing relative displacement of subannules. 64. Surface view of two annules showing relative displacement and widening of inner subannule. 65. Reconstruction of one annule about middle of body. 66-72. *Parapinnanema wilsoni*. 66. Anterior

MALE: gubernaculum with L-shaped lateral pieces; elongate, narrow, thickened. mid-ventral pre-cloacal cuticular modification; tail long and slim.

TYPE SPECIES: *Parapinnanema wilsoni* sp. nov.

PROTOCHROMADORA gen. nov.

Euchromadora scampae Coles, 1965 is characterized by an intermediate circle of six non-setase cephalic sense organs and four setae in the outer circle. The dorsal onchium is apparently hollow in some specimens and apparently solid in others (Text-figs. 48, 50). However the oesophastome has no denticles along the anterior dorsal edge, there are two ventral cone-like onchia and there is no trace of any lateral oesophastomal modification of any kind, neither in the forms of transverse rows of denticles nor as lateral flanges (Text-fig. 47).

The cuticle just posterior to the outer circle of cephalic sense organs is marked by tiny, slightly elongate, punctations which become more prominent posteriorly. They are large oval punctations over the anterior half of the length of the oesophagus which lie directly within the annulations. In other words, on focusing down through the annules the punctations lie directly over the inner sub-annules and wholly below the outer sub-annules so that there is no appearance of movement.

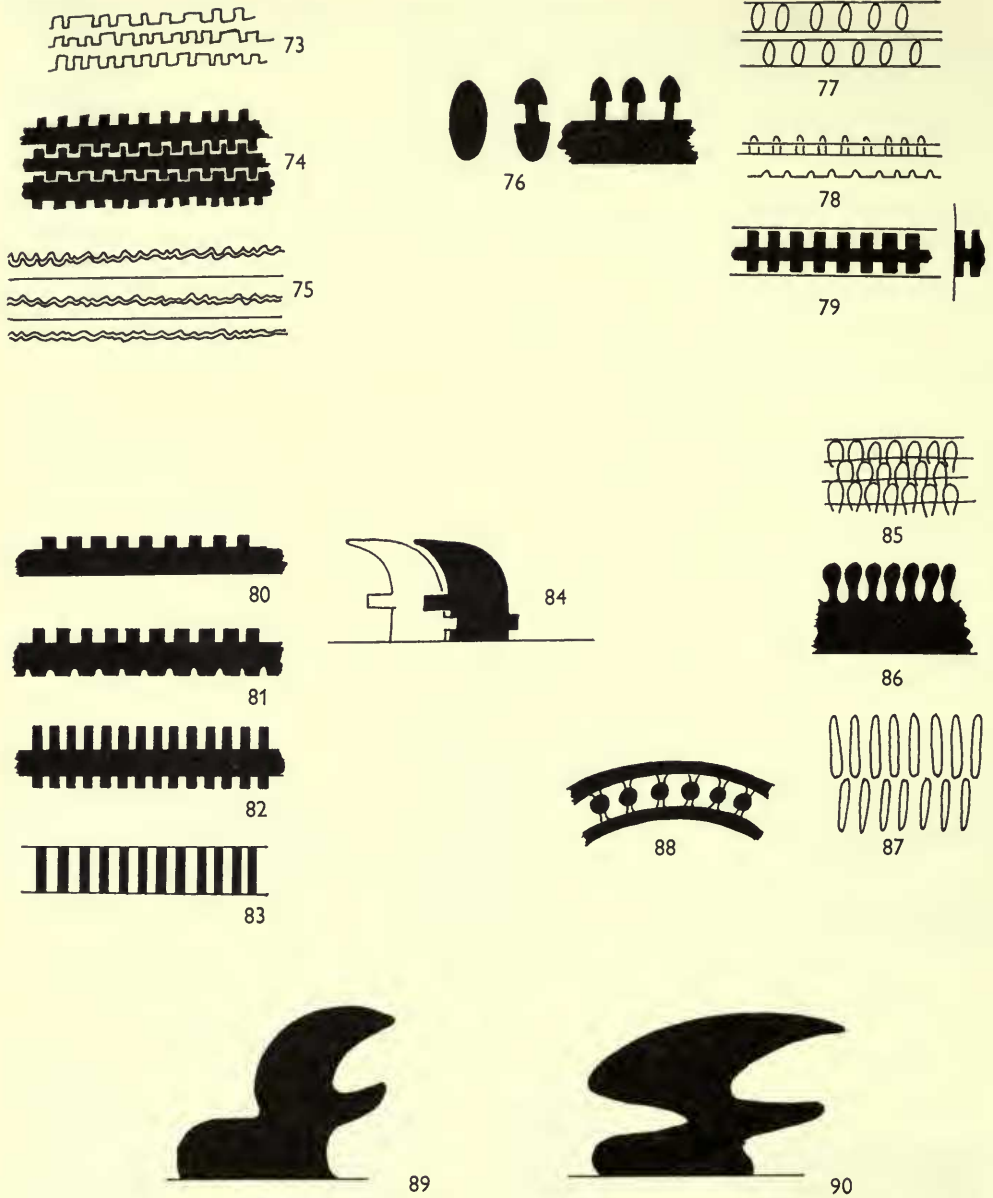
The punctation blocks are not, however, simple in structure since on focusing through them, from the surface, they become somewhat dumb-bell-shaped in section and finally at the deepest level are battlement-like in appearance (Text-figs. 76-79). The punctation blocks become slimmer on studying them more posteriorly and become much less prominent, very slim and close together. At the same time they begin to project from the anterior edge of each annule. As this projection becomes more pronounced notches appear in the posterior edges of each annulation to accept the processes projecting from the next more posterior annule (Text-figs. 77, 78). These notches on the posterior edge become deeper and more pronounced until the annules appear to be battlemented on both their edges (Text-fig. 79) with a distinct transverse striation running between them. I am not certain at which level these punctations lie within the cuticle but those on the anterior end appear due to processes in the middle depth while those on the middle of the body appear to be due to indentations on the extreme outer subannule of the cuticle (Text-fig. 79).

The conditions are reversed over the posterior half of the body.

Tiny lateral plates are present starting on the anterior end of the body about the

FIGS. 60-72—contd.

end of body, surface view. Black region is outer surface, white processes lie inwards. 67. Reconstruction of anterior annule. 68. Dorso- and ventro-lateral articulating processes. 69-72. Annules in longitudinal section, anterior to left. 69. Thick cuticle over anterior region of oesophagus. 70. Middle of oesophagus length, posterior process displaced outwards. 71. Posterior end of oesophagus. posterior process now on outer surface, anterior processes replaced by grooves on anterior edge. 72. One-third of body length from anterior end. Note distortion of annules with dominance of inner system of processes; outer processes reduced to irregularities on outer edges of annules.



FIGS. 73-90. 73-75. *Parapinnanema wilsoni*: surface appearance of cuticle. Anterior end towards top. 73. Just posterior to amphids. 74. Over oesophagus length. 75. On most of body posterior to oesophagus. 76-79. *Protochromadora scampae*: cuticle. 76. Punctuation just posterior to amphids. From left to right: surface, about middle level, deep view (see description, page 177). 77. Just posterior to amphids. 78. Over first quarter of oesophagus. 79. Over most of body, plan on left, longitudinal section on right. 80-84. *Graphonema georgei*: surface appearance of cuticle. 80. Just posterior to amphids. 81. Three annules posterior to 80. 82. First third of oesophagus

level of the middle of the length of the oesophagus but over the middle region of the body they are represented by a series of granulations lying between the innermost parts of the dense annules of the cuticle.

The cuticle is marked by punctations laterally, but is clear dorsally and ventrally over the middle length of the body. In the male there is no precloacal mid-ventral modification of the cuticle and the tail is relatively short and stout.

This species is obviously distinct from those grouped in the genera *Euchromadora* and *Steineridora* and I propose to refer it to a new genus the validity of which will become clearer below.

PROTOCHROMADORA gen. nov.

Chromadoridae.: CUTICLE: complex with large, prominent, elongate punctations anteriorly and posteriorly which appear to correspond to processes developed on one side of each annule only; similar, but slimmer, punctations restricted to lateral surfaces of body over much of middle length; cuticle without punctations dorsally and ventrally over similar middle length of body; "lateral plates" represented by granules.

HEAD: dorsal onchium possibly solid but impossible to classify rigidly; no denticles on anterior dorsal edge of oesophastome; no denticles or flanges or any other structures on lateral walls of oesophastome; one cone-like, anteriorly directed onchium on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which outer consists of four setae; mouth surrounded by twelve rugae; amphids elongate, transverse slits, not bordered by prominent fringes of cuticle; oesophagus without prominent posterior bulb.

MALE: gubernaculum with L-shaped lateral pieces; no pre-cloacal supplements or other modification of cuticle; tail relatively short and stout.

TYPE SPECIES: *Euchromadora scampae* Coles, 1965.

OTHER SPECIES: *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958).

The reference of *E. mediterranea* Allgén 1942 to *Protochromadora* is based on a study of some specimens in a rather poor condition. Nevertheless it is possible to confirm their specific identity and to establish with a fair degree of certainty their similarities to *P. scampae*.

The inclusion of *Euchromadora parafricana* Gerlach, 1958 in *Protochromadora* is slightly less certain as it is based on the published description. Gerlach (1958) gives

FIGS. 73-90—contd.

to first third of body length. 83. Remainder of body. 84. Longitudinal section, about level of figure 82. Anterior to left. 85-88. *Austranema shirleyae*: cuticle. 85. Surface appearance, anterior end of body. 86. Detail at same level as 85. 87. Body posterior to oesophagus. 88. Transverse section at same level as 87 showing origins of punctation processes. 89. Longitudinal section at anterior end. Note marked anterior displacement of outer subannule. 90. Longitudinal section about middle of body (anterior to right in 89 and 90).

two figures of the head, one of which shows a hollow dorsal onchium (Gerlach, Fig. 4a) while the other (4b) shows a possibly hollow or solid dorsal onchium, reflecting the difficulty of distinguishing between the two forms. In addition an intermediate and an outer circle of setae is shown in Fig. 4b while only an outer circle of four setae is shown in Fig. 4a. The tail is long and thin, there are no pre-cloacal modifications or supplements and the oesophagus does not end in a bulb. The illustrations of the cuticle suggest the condition in *P. scampae* and I refer *E. parafricana* to *Protochromadora* with little hesitation.

GRAPHONEMA Cobb, 1898

Graphonema Cobb, 1898 is, in some ways, the most distinctive genus which remains to be considered and was erected by Cobb (1898) for *G. vulgaris* Cobb, 1898 with a reference to a further forthcoming species, *G. pachyderma*, which was never described. *G. vulgaris* was based on specimens collected from algae and sea sand on the coasts of New South Wales and Victoria, Australia. In describing it Cobb specifically draws attention to the following points: "The conoid neck terminates in a truncate head, conspicuous because of a distinct constriction behind it, and because of the sudden diminution in size on it of the cuticular markings . . ."; "The six cephalic setae opposite the apex of the dorsal tooth, and the four sub-cephalic setae . . .". In addition he refers to a minute dorsal tooth; linear, arcuate spicules of equal width throughout their lengths; a gubernaculum with lateral pieces; no oesophageal bulb and no pre-cloacal supplements.

I have collected specimens from the west coast of Australia, described below, which conform to this description with very great accuracy in all respects, although they appear to represent a different species from that described by Cobb (1898). As a consequence it is possible to reassess the status and diagnosis of the genus *Graphonema*.

The genus is easily recognized because the head is, as reported by Cobb, distinctly set-off as a swollen, almost globular, region on which there are very fine dot-like punctations (Text-fig. 28). More posteriorly the cuticle becomes thicker over the region of the oesophagus but always remains relatively thin and delicate in appearance when compared to the conditions in *Euchromadora* and the other genera considered here. Nevertheless the annulation of the cuticle is fairly marked and obvious. The punctations at the anterior end of the body, just posterior to the swollen region, are of a definite battlement-like form although the battlement processes are small relative to the width of the annules from which they arise (Text-fig. 80). On passing posteriorly the processes rapidly increase in relative size and notches develop in the posterior edges of the annules of dense material (Text-fig. 81). By the level of the posterior end of the first third of the length of the oesophagus the annules bear a distinct system of double battlement-like processes. The processes on the anterior edge are longer and nearer the surface of the cuticle than those on the posterior edge (Text-figs. 82, 84). Over the whole of this region the annules of dense cuticular material are roughly rectangular in longitudinal section with slight flanges developed along their anterior edges (Text-fig. 84).

The double-battlement markings on the cuticle over the posterior two-thirds of the oesophagus continue over the region posterior to the oesophagus virtually unchanged until about one-third of the total body length from the anterior end of the body where the battlement-like processes on the posterior edge of the annules move relatively nearer the surface of the cuticle, the cuticle becomes thinner and the punctations now look like long thin blocks (Text-fig. 83).

There are four clear zones running down the cuticle on the dorso- and ventro-lateral aspects so that the cuticle is marked by punctations dorsally and ventrally along the whole length of the body. These punctations are thinner and less obvious than those occurring on the lateral surface of the body. In the males there is no mid-ventral pre-cloacal modification of the cuticle and the gubernaculum is small and slightly L-shaped.

The mouth opening is surrounded by the usual twelve rugae and the cephalic sense organs are in three distinct circles of which the members of the outermost two circles are setose (Text-fig. 29). The amphids are very prominent, transverse slits bordered by obvious thin fringes of cuticle which stand out from the general surface of the cuticle. The circles of cephalic setae are far apart and the members of the outer circle lie on the same level as the amphids which are themselves positioned relatively far posteriorly from the anterior end of the body.

The dorsal onchium is small, hollow, directed anteriorly and there are no denticles developed on the anterior dorsal edge of the oesophastome. Each of the lateral walls of the oesophastome bears a flange which projects anteriorly most markedly towards its dorsal edge so that it resembles an anteriorly directed onchium when the level of focus is high. However on focusing down through the head, in an *en face* preparation, the flange appears progressively. There are no distinct separate denticles or processes developed from the effectively continuous edge of the flange (Text-fig. 30).

Each ventral sector bears one fairly prominent cone-like onchium. There is another less prominent pair, each member of which arises from, or near to, the ventro-lateral corners of the oesophastomal funnel. These structures are definitely present (Text-fig. 30) and there is a possibility that each ends anteriorly as a double point. This cannot be established with certainty but when this head is studied *en face* the dentition of the oesophastome is immediately obvious as seven bright points of light (Text-fig. 29) of which one is large and dorsal (the dorsal, anteriorly pointing onchium), two fairly large are lateral in position (representing the anterior edges of the lateral flanges), and four occur in an almost straight line across the ventral wall of the oesophastome (the onchia on the ventral sectors and those arising from the ventral corners of the oesophastome). With more careful focusing and studying the less certain second points to the ventro-lateral onchia can be made out.

The oesophagus expands evenly posteriorly but there is no distinct posterior bulb. The tail is long and slim (Text-fig. 99).

These features conform so exactly to Cobb's verbal picture of *G. vulgaris* that there can be little doubt that we are dealing with a species which is at least congeneric. As a consequence it is possible to reassess the genus which is certainly distinct.

The discovery of unequivocal specimens of *Graphonema* has further taxonomic

consequence since Wieser (1954) “. . . thinks I am able to revive Cobb's doubtful genus . . .” and refers four species to that genus while in 1959 he adds another four species of which two are new.

As a result the genus currently contains the following nine species in addition to the type species: *Chromadora sabangensis* Steiner, 1915; *Spilophora amokuroides* Allgén, 1927 (redescribed by Wieser, 1954); *Spilophora norvegica* Allgén, 1932; *Chromadora paraheterophya* Allgén, 1932; with *Spilophora pusilla* Allgén, 1947; *Chromadora suilla* Allgén, 1947 and *Chromadora spectabilis* Allgén, 1932 referred to the synonymy of these species (Wieser, 1954); in 1959 Wieser adds the following species: *G. flaccida* Wieser, 1959; *G. clivosa* Wieser, 1959; *Chromadora tentabunda* de Man, 1890; *Chromadorita crassa* Timm, 1952 and *Chromadorita chitwoodi* Wieser, 1954.

However of these species *Chromadora tentabunda*, which is redescribed by Gerlach (1951), has a simple gubernaculum without L-shaped lateral pieces, a post-oesophageal bulb, a prominent hollow dorsal onchium with a well developed dorsal expansion of the oesophagus associated with it, the head is not set off and the intermediate circle of cephalic sense organs is not setose. Timm's (1952) *Chromadorita crassa*, a new name for *C. tentabunda* of Chitwood (1951), is I agree with Wieser (1959) almost certainly de Man's species.

Both *G. flaccida* and *G. clivosa* have a similar combination of characters; the dorsal onchium is large and hollow, the intermediate cephalic sense organs are not setose, there is a posterior oesophageal bulb, the gubernaculum lacks lateral pieces and the heads are not set off.

Spilophora amokuroides Allgén, 1927 is redescribed by Wieser (1954) and referred to the genus *Graphonema* with *S. pusilla* Allgén, 1947 and *Chromadora suilla* Allgén, 1947 as synonyms. As Wieser (1954) points out, Allgén's descriptions of *S. amokuroides* and *S. pusilla* are “insufficient” and he later (Wieser, 1959) adds that the use of the name *S. amokuroides* for his redescription is “. . . hypothetical, since Allgén's inexact figures and descriptions could very well fit any species of this group.” I concur and propose to rename *Graphonema amokuroides* of Wieser, 1954 and will treat all four of Allgén's species as *species dubia*.

Chromadora sabangensis Steiner, 1915 is referred to *Graphonema* by Wieser (1954) but is originally described from females which makes discussion difficult. The intermediate circle of sense organs is not setose, the dorsal onchium is small and hollow, the punctations on the anterior end of the body are very light or lacking, the punctations on the general surface are thin and elongate and the posterior end of the oesophagus does not form a distinct bulb. It is, at best, a *species inquirendum*.

Finally *Spilophora amokuræ* Ditlevsen, 1921 as redescribed by Wieser (1954) under the name *Euchromadora amokuræ* and according to the original description, has a clear zone of cuticle anteriorly, the dorsal onchium is hollow, the intermediate circle of cephalic sense organs appears to be setose, there is no report of any pre-cloacal modification of the cuticle on the ventral surface of the male, the lateral pieces of the gubernaculum are L-shaped, and the tail is long and slim. In many of these respects the species differs from those referred to *Euchromadora* and, although some doubt remains, it appears most probably referable to *Graphonema* as re-diagnosed.

The redescription of a *Graphonema* species, *sensu* Cobb, means that the species referred to that genus by Wieser are displaced and I propose to refer them to a new genus, *Innocuonema*. This new genus and *Graphonema* may be differentially diagnosed thus:

GRAPHONEMA Cobb, 1898

Chromadoridae: CUTICLE: anterior end of body swollen, bulb-like without punctations anteriorly and with tiny dot-like punctations posteriorly; anterior punctations, just posterior to bulb region, prominent and battlement-like; more posteriorly punctations long and slim; punctations on both dorsal and ventral surfaces of body; dorso- and ventro-lateral strips of articulating processes.

HEAD: markedly set off as swollen, bulb-like region; dorsal onchium hollow; no denticles on anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome, without dentate anterior edges; two prominent, cone-like anteriorly directed onchia on each ventral sector at base of oesophastome; cephalic sense organs in three circles of which intermediate and outer are far apart and composed of setae; mouth surrounded by twelve rugae; amphids prominent transverse slits bounded by prominent fringes of cuticle; oesophagus without prominent posterior bulb;

MALE: gubernaculum with poorly developed L-shaped lateral pieces; no pre-cloacal supplements or other modification of cuticle; tail long and slim.

TYPE SPECIES: *Graphonema vulgaris* Cobb, 1898.

OTHER SPECIES: *G. georgei* sp. nov.; *G. amokuræ* (Ditlevsen, 1921).

INNOCUONEMA gen. nov.

Chromadoridae: CUTICLE: punctations complex and obvious; no lateral differentiation; no other information available.

HEAD: head not set off as swollen region; dorsal onchium fairly obvious and hollow, with associated dorsal swelling of oesophagus; structure of oesophastome unknown; only outer circle of four sense organs setose; amphid not prominent; definite posterior oesophageal bulb.

MALE: gubernaculum without prominent lateral pieces; no pre-cloacal supplements or other pre-cloacal modifications; tail long and slim.

TYPE SPECIES: *Graphonema flaccida* Wieser, 1959.

OTHER SPECIES: *I. clovosa* (Wieser, 1959); *I. tentabunda* (de Man, 1890); *I. chilensis* nom nov pro *Graphonema amokuroides* of Wieser, 1954 non *Spilophora amokuroides* Allgén, 1927.

The following species are considered *dubia*: *Chromadora suilla* Allgén, 1947; *C. paraheterophya* Allgén, 1932; *Spilophora norvegica* Allgén, 1932; *S. amokuroides* Allgén, 1927; *S. pusilla* Allgén, 1947 and *Chromadora spectabilis* Allgén, 1932.

NYGMATONCHUS Cobb in Cobb, 1933

Before considering the remaining *Euchromadora*-type species I have seen it is necessary to consider the delimitation and diagnosis of the genus *Nygmatonchus* Cobb in Cobb, 1933. This genus was erected with one contained species, *N. scriptus* Cobb in Cobb, 1933, which was described, without illustrations, by reference to the genus *Rhips* Cobb, 1920. Using a combination of the verbal description of *N. scriptus* and the illustrations of *Rhips ornata* Cobb, 1920 it is possible to establish the following characteristic features for *Nygmatonchus*. The dorsal onchium is small, hollow and anteriorly directed, the amphid is prominent with a double contour, the cuticle is complex with lateral differentiation and basket-work markings anteriorly but only dots about the middle of the body, the cephalic sense organs of the intermediate and outer circles are setose and lie at the same level, the oesophagus lacks a definite posterior bulb, the tail is long and slim, and there is possibly a region of raised pre-cloacal modification on the males (not mentioned by later authors).

Wieser (1954) describes a new species *N. fossiferus* but delimits *Nygmatonchus* as "Distinguished from *Neochromadora* by having ten instead of the usual four cephalic setae". As the descriptions in this paper show, such a condition obtains in a wide range of forms. Nevertheless Wieser's description agrees with that given by Cobb in Cobb (1933) fairly well although the amphid is not obviously like that of *Rhips*, and the gubernaculum is not obviously L-shaped as in *Rhips*, a condition suggested by Cobb in Cobb's description.

Andrassy (1959) describes what he considers to be a female of *Nygmatonchus scriptus* and although I consider it unestablished that it is referable to that species it is, nevertheless, recognizably the same genus. Here, also, the dorsal onchium is small and hollow, the intermediate and outer circles of setae occur at the same level, the amphid is prominent with a double contour, there is definite lateral differentiation of the cuticle, and the tail is long and slim. Most recently Gerlach (1967) describes a new species *N. minutus*, in which the cephalic setae are in two circles but which otherwise agrees with the diagnosis of the genus.

These characters may be summarized in a diagnosis as:

NYGMATONCHUS Cobb in Cobb, 1933

Chromadoridae: cuticle complex anteriorly, elongate punctations posteriorly on middle of body; distinct lateral differentiation; intermediate and outer circles of cephalic sense organs on one or two levels, setose; amphid prominent with double contour; oesophagus without definite posterior bulb; dorsal onchium small and hollow; tail long and slim.

MALE: pre-cloacal modification on male (?); gubernaculum not L-shaped.

TYPE SPECIES: *Nygmatonchus scriptus* Cobb in Cobb, 1933.

OTHER SPECIES: *N. fossiferus* Wieser, 1954; *N. bicornata* (Wieser, 1959) comb. nov.; *N. minutus* Gerlach, 1967.

The reference of the three latter species to the genus is slightly doubtful. Although the first appears to be a true member of the genus the illustration of the amphid given by Wieser (1954) does not match that described by Cobb since it is short and rather indistinct (compare Wieser's Fig. 141a of *N. fossiferus* with Fig. 142a of *Actinonema pachydermatum* Cobb, 1920 a much more *Rhyps*-like amphid), and Wieser, as Murphy (1965) points out, does not mention any pre-cloacal modification of the cuticle.

Neochromadora bicornata was described by Wieser (1959) from females only so that it is difficult to refer it to any genus with certainty, but here again the amphid is small and indistinct, and the cephalic sense organs of the intermediate and outer circles are setose. Nevertheless the structure of the cuticle appears to match that of *Nygmatochus*, particularly when Andrassy's (1959) and Gerlach's (1967) illustrations are considered, and I will refer Wieser's species to *Nygmatochus* as a provisional measure, at least until males have been described.

Murphy (1965) describes a new species *Nygmatochus alii* of which he says "My species conforms so closely to Cobb's generic description that there is little room for doubt as to generic placement". (Murphy, 1965; page 208.) However, the discovery of several species with roughly the same combination of characters as *N. alii* raises difficulties since if Wieser's interpretation of *Nygmatochus* is correct and his illustration of the gubernaculum accurate the genus is characterized, among other features, by a small *Neochromadora*-type gubernaculum while if Murphy is correct the gubernaculum is *Euchromadora*-like.

However Cobb in Cobb's (1933) description of *N. scriptus* does not say that the lateral pieces of the gubernaculum (telamons) resembles those of *Rhyps* (which are L-shaped) which one might have expected in view of the other direct reference to that genus. I, therefore, continue to accept Wieser's (1954) interpretation of the genus and cannot accept that Murphy's species is referable to it, particularly as the lateral differentiation he illustrates is not lateral and does not suggest "wings" as mentioned by Cobb in Cobb (see below, page 200).

AUSTRANEMA gen. nov.

The remaining *Euchromadora*-like species I have studied are all characterized by the presence of flanges, developed from the lateral walls of the oesophastome, with dentate anterior edges; the cephalic setae are in one circle of ten and lie anterior to the level of the amphids; the amphids are wide and prominent with cuticular fringes; the dorsal onchium is generally hollow; the cuticle is thick over the oesophageal region of the body; the lateral pieces of the gubernaculum are L-shaped; the tail is long and slim; there is a region of pre-cloacal modification on the mid-ventral surface of the body in the form of a raised strip of cuticle; the cuticle is marked by punctations dorsally and ventrally; the posterior end of the oesophagus swells evenly but there is no distinct posterior bulb; there are no denticles along the dorsal anterior edge of the oesophastome and there are anteriorly directed, cone-like onchia ventrally within the oesophastome.

Nygmatochus alii Murphy, 1965 falls neatly into this group and the only apparent discrepancies are that Murphy does not report any dentition on the anterior edge of the lateral flanges of the oesophastome, although he illustrates the presence of such flanges in optical section (Murphy, 1965, Fig. 1, D) and describes a definite lateral differentiation of the cuticle. However, I have a few specimens from Western Australia which appear to be indistinguishable from those described by Murphy and can establish that the lateral oesophastomal flanges are dentate and that there is no lateral differentiation. I suspect that Murphy has, instead, illustrated the dorso- and ventro-lateral files of articulating plates common on this kind of nematode.

Similarly a re-examination of the original specimens of *Euchromadora shirleyae* Coles, 1965 and *E. colesi* Inglis, 1968 shows them to have this combination of characters and, to that extent, cannot remain as members of the genus *Euchromadora* (The description of the cephalic sense organs of *E. colesi* in Inglis (1968) is wrong.) It may be stressed again that when the mouth opening is closed and the oesophastome somewhat collapsed, the dorsal onchium folds posteriorly upon itself and gives every appearance in lateral view of being solid. However, when the mouth is open and the dorsal onchium fully extended it is clearly hollow.

I have been able to study the cuticle in some detail in *E. colesi*, *E. shirleyae* and *N. alii*, and it is structurally the same in all three. The sole difference of note is that the punctuation blocks are much larger and the cuticle is thicker in *E. shirleyae* than in *N. alii* and *E. colesi*. As a result most of the following description is based on *E. shirleyae*. The structure of the cuticle in these three species differs from that in all the other species described in this paper in that each annule of dense material, when studied in transverse section, is markedly skewed, even at the extreme anterior end of the body so that the outer sub-annule lies fairly far anterior to the innermost (Text-fig. 89). This condition continues over the whole length of the body with the conditions reversed on the posterior half, i.e. the outer sub-annule is then posterior relative to the innermost.

The cuticle for about one head diameter posterior to the anterior end is marked by simple, dot-like punctations and then elongate punctations appear which are, as usual, due to the presence of anteriorly directed processes lying in the middle level of the cuticle. Initially these punctuation-blocks are restricted to the anterior edge of each annule to give the appearance of a battlement-like cuticle (Text-figs. 85, 86) but after only two or three annules the punctations become elongate rectangles when viewed from the surface (Text-fig. 87). When single annules are studied, however, the punctations do not lie as strips in one plane but appear to be higher anteriorly than they are posteriorly. This appears to be caused by the anterior half (approximately) of each punctuation being produced by the anteriorly directed process while the posterior half is due to grooves in the innermost, relatively posterior, sub-annule (Text-fig. 89). The processes are, as in *Euchromadora*, circular in transverse section and, although completely free nearer their outer ends, attached to the surface sub-annule by a thin strip of cuticle while more posteriorly a second similar strip attaches them to the innermost sub-annule (Text-fig. 88). As a result there are channels running through each annule between the punctuation processes which continue as grooves in the innermost sub-annule.

Steiner & Hoespli (1926) create a new genus *Dicriconema*, for a new species *D. tenuis*, based on the study of "... an apparently young female ..." from Japan. The genus was diagnosed largely on the structure of the cuticle and, although both Wieser (1954) and De Coninck (1965) treat it as a "solid toothed" form, the original authors give no explicit information about the structure of the dorsal onchium and their figure (Tafel 1, Fig. 1) suggests that it was in fact hollow. The description shows that the cuticle is marked by elongate punctations over the whole surface, except for dorso- and ventro-lateral strips, and it appears possible that they studied a specimen similar to those discussed here.

I prefer not to use the name *Dicriconema* because it is extremely doubtful that *D. tenuis* could ever be unequivocally recognized. The difficulty is that mentioned in discussing *Odontocricus*. It is not yet possible to be sure that the structure of the cuticle is always covariant with the same features of other parts of the animal and, even if this could be established, it is doubtful that *D. tenuis* could ever be anything other than a *species inquirenda*, as I propose to treat it. It therefore appears advisable, because fairly drastic changes are involved anyway, that the knot be cut by introducing a new name for a generic group containing *E. shirleyae*, *E. colesi*, *N. alii* and related species.

AUSTRANEMA gen. nov.

Chromadoridae: CUTICLE: small, elongate punctations anteriorly which are not obviously battlement-like on all specimens but which are due to processes within cuticle developed from both sides of annules; cuticular annules markedly skewed anteriorly and posteriorly; punctations present on dorsal and ventral surfaces, although sometimes slimmer than those laterally at same level; dorso- and ventro-lateral files of articulating processes;

HEAD: not obviously set off; dorsal onchium difficult to classify but usually hollow; no denticles along anterior dorsal edge of oesophastome; flanges on lateral walls of oesophastome with dentate anterior edges; prominent, cone-like, anteriorly directed onchia on ventral sectors at base of oesophastome; outer and intermediate circles of cephalic sense organs at same level, all setose; mouth surrounded by twelve rugae; amphids prominent, transverse slits bounded by prominent cuticular fringes; oesophagus without posterior bulb, but slightly expanded posteriorly.

MALES: gubernaculum with prominent L-shaped lateral pieces; mid-ventral, elongate, pre-cloacal modification present; tail long and slim.

TYPE SPECIES: *Euchromadora colesi* Inglis, 1968.

OTHER SPECIES: *A. shirleyae* (Coles, 1965); *A. alii* (Murphy, 1965); *A. pectinata* (Wieser & Hopper, 1967).

Euchromadora pectinata Wieser & Hopper, 1967 is described as having a pre-cloacal mid-ventral modification of the cuticle and an oesophagus with a dilated posterior end but no distinct bulb; but the intermediate circle of cephalic sense organs is papillose. I shall, therefore, refer it to *Austranema* because of the first two features and full confirmation must depend upon a re-examination of the specimens. It

should be noted that Wieser & Hopper (1967) refer to the presence of a post-cloacal thickening of the cuticle. This kind of modification occurs in some specimens of all the species I have seen but does not appear to be consistent in its occurrence. Perhaps I have simply been unable to see it.

Euchromadora meadi Wieser & Hopper, 1967 is left in the genus *Euchromadora* although it looks suspiciously like a member of *Austranema*. Here again a re-examination of the specimens is called for.

Uncertain *Euchromadora* and *Euchromadora*-like Species

Some nominal species which have been described as members of *Euchromadora* and some species which appear similar to the various genera recognized above remain to be considered. Some of these species may be easily dismissed because of poor descriptions but others have to be considered because the convergence demonstrated above makes their generic placement difficult or uncertain. In such cases there is little doubt that the species concerned could be recognized again but there is insufficient information at present to allow them to be referred to one or other of the *Euchromadora*-like genera recognized here.

Cobb (1914) describes four new species from the Antarctic, which he refers to *Euchromadora*. More recently two of them are referred to other genera by Wieser (1954): *E. antarctica* to *Prochromadorella* and *E. septentrionalis* to (?) *Hypodontolaimus*; while the other two *E. denticulata* and *E. meridiana*, are kept in *Euchromadora* as doubtful species which are treated as *species dubiae* by Coles (1965). While agreeing with this, it is worth pointing out that it is now clear that neither of these latter species is a *Euchromadora*-type. Both have "hollow" dorsal onchia, both have two circles of setae, both have very prominent amphids and both have extensive, non-punctate or lightly punctate regions anteriorly. Unfortunately the descriptions make it impossible to establish their relationships more fully and it remains doubtful that either could be recognized again.

A large number of nominal species of *Euchromadora* have been named, described, redescribed or reported by Allgén in a large number of publications. Some of these have been "recognized" and redescribed by other authors but the general standard of Allgén's work is so poor that many such redescriptions are based on guess work. The majority of Allgén's species have been treated as unrecognizable by several authors (summarized by Coles, 1965), and will not be reconsidered here.

Steiner (1918) describes five new species of *Euchromadora* all of which are best treated as *dubia*, as proposed by Coles (1965) who, however, treats *E. hupferi* as a *species inquirenda*. As argued above, although it is possible to recognize the genus to which this species should be referred it is most unlikely that the species could ever be recognized. As a consequence *E. hupferi* is also considered a *species dubia*.

It is worth noting that *E. longicaudata* Steiner, 1918, in which the amphid is prominent with, apparently, a double contour and a dorsal onchium which appears to be of the hollow-type, is referred to *Actinonema* by Wieser (1954). Wieser, nevertheless, points out that "the male genital apparatus of this species is insufficiently described but it clearly differs in structure from that of the following species."

(i.e. *A. pachydermatum* Cobb, 1920). This is certainly not true since Steiner only studied a female and naturally says nothing about the male and it is extremely unlikely that Steiner's species could be unequivocally recognized again or differentiated from other species of any genus to which it might be thought to belong.

Wieser's (1954) comment on *A. longicaudata* must refer to the descriptions of *Pareuchromadora fragilis* of Allgén, 1942 and *P. setifer* Schuurmans Stekhoven, 1943 both of which he refers to the synonymy of *E. longicaudata*. There is no obvious justification for any of this since *P. fragilis* is, like *E. longicaudata*, known only from a female while *P. setifer* is recognizably an *Actinonema* species. As a consequence I treat *E. longicaudatum* Steiner, 1918 as a *species dubia*; *P. fragilis* of Allgén, 1942 as a *species dubia* and recognize *P. setifer* as a *species inquirenda* and refer it to *Actinonema*.

Also in 1943 Schuurmans Stekhoven describes *Euchromadora inflatispiculum* which is clearly not referable to that genus and must remain a species *incertae sedis* until further specimens have been studied. From the descriptions it appears to have a hollow dorsal onchium and the redescription of Schuurmans Stekhoven (1950) does not appear to be the same species as that described in 1943, as is pointed out by both Wieser (1954) and Coles (1965).

Euchromadora arctica Filipjev, 1946 is a species with a hollow dorsal onchium, an oesophagus without a posterior bulb, with L-shaped lateral pieces to the gubernaculum, four cephalic setae, an extensive clear zone of cuticle at the anterior end of the body and, according to Filipjev (1946), there is a mid-ventral pre-cloacal papilla on the male. If this be correct the species is very different from any of the others described here or by others. In addition the form of the dorsal onchium is very cyatholaimid in appearance. As a result I propose to treat this species as *incertae sedis* although it shows some similarity to *Austranema*.

REMARKS ON THE CLASSIFICATION OF THE CHROMADORIDAE

Almost all discussion of the classification of free-living marine nematodes, in particular, and all non-parasitic forms in general, starts or finishes by stressing the doubtful value of much of the present grouping. Such comments are undoubtedly justified. The classification of the Family Chromadoridae is no exception and is probably as unreliable as that of any other family. Its limits and divisions float in a cloud of taxonomic uncertainty lightened only by flashes of morphological ignorance. As De Coninck says, "Toute la famille des Chromadoridae devra etre soigneusement révisée" (De Coninck, 1965, page 637.)

Although it is easy to offer destructive criticism of the classification, constructive suggestions are much more difficult to formulate because of our extensive lack of knowledge about the animals involved. The weakness of this position is well exemplified by the present work. It is only too clear that there is no sound basis on which to erect a classification; and there is no background of morphology against which to assess new information. The immediate consequence is that it is difficult to suggest easily observed characters or, more usefully, characters which have previously been described, which can be relied upon to be covariant with those structures of the head and cuticle described above.

The recognition of one group with a solid dorsal onchium and one with a hollow onchium is easy when the extreme and clear cut conditions are compared. The division is difficult, if not impossible, to apply when a solid "hollow" onchium is examined. Equally the two groups, so far as they have been studied, appear to differ in several covariant characters of the cuticle and dentition but it is difficult to apply this to those groups with simple punctate cuticles and we do not know, as yet, whether all the "hollow" toothed forms are similar in their other morphological characters. In other words it has been established that some "solid" toothed forms are, in other characters, most similar to "hollow" toothed but we do not yet know if forms which look obviously "hollow" toothed may not later be found to have great similarities with the obviously solid toothed.

In an attempt to overcome some of this uncertainty I have looked at a very small number of other species. In *Spilophorella paradoxa* (de Man, 1888), for example, there is obvious difficulty in describing the structure of the dorsal onchium. I would call it hollow but most groupings presuppose it is solid (e.g. Wieser, 1954; De Coninck, 1965). Be that as it may, there is a pair of small, ventral, anteriorly directed cone-like onchia in the oesophastome and there appear to be lateral flanges arising from the lateral oesopharhabdions. In these respects, therefore, *Spilophorella* falls into the hollow-toothed group of genera.

The conditions in *Hypodontolaimus* are much clearer, because the specimens of *H. slacksmithi* (described below) are relatively large. Here the mouth is surrounded by twelve, inwardly pointing, flanges developed from the wall of the cheilostome and there are no rugae as in typical Chromadoridae, the dorsal onchium is very prominent and hollow, there are no denticles along the dorsal anterior edge of the oesophastome, the oesophastome is rectangular in transverse section with two ventral, cone-like, anteriorly directed onchia on the ventral sectors and there are typical lateral flanges developed from the lateral walls of the oesophastome. These flanges are most anterior towards their ventral edges so that they look like pointed onchia on focusing up on *en face* preparations (Text-figs. 57-59).

In addition, in *Hypodontolaimus* the cuticle is of a battlement-type and a similar condition is suggested for various other "hollow" toothed species. For example Filipjev's (1918) illustrations of *Chromadora sabulicola* (Plate 8, fig. 50b) and *C. poecilosomoides* (Plate 8, figs. 52a, b, c) [both now referred to *Neochromadora*] show a battlement-like cuticle co-occurring with a hollow dorsal onchium. Equally many of Gerlach's (1951) illustrations show a similar association between a hollow onchium and a battlement-like cuticle.

To extrapolate, it appears that the presence of a hollow dorsal onchium is frequently associated with the presence of lateral flanges and cone-like ventral onchia in the oesophastome, and with the possession of a battlement-like modification of the dense component within the cuticle. There is, as yet, insufficient information on the structure of the cuticle and oesophastome in those species with an unequivocally solid dorsal onchium to allow any conclusions to be reached and the relationships of those species with simple punctate cuticles may always be difficult to establish. In spite of this uncertainty it appears that Wieser's (1954) treatment of the Chromadoridae in two groups distinguished crudely by the form of the dorsal

onchium is of significance but it is doubtful that enough information yet exists to make De Coninck's (1965) division of the family into subfamilies on the same character acceptable.

For example there appear to be at least two distinct groupings possible for those genera in which the dorsal onchium is hollow. One of the groups consists of the genera considered above, which appears to culminate in a form such as *Parapinnanema wilsoni*, in which the cuticle is elaborate, thick and strong but the dorsal onchium is small. The other group contains those nematodes in which the dorsal onchium is very prominent and obviously hollow, frequently with a massive development of the oesophageal musculature associated with it, the cuticle is not thick, very elaborate and dark, and the gubernaculum is relatively simple. This group contains genera such as *Hypodontolaimus* and *Nygmatochus*.

I would, therefore, expect that further study will lead to the recognition of at least three distinct groups within the subfamilies Chromadorinae and Hypodontolaiminae as recognized by De Coninck (1965). This does not, however, take into consideration those forms grouped by De Coninck in the Ethmolaiminae, Cyatholaimidae and even the Desmodoridae, the analysis of whose relationships is closely tied to the Chromadoridae. In all these groups there appear to be various independent lines of modification all of which lead to a stronger and more elaborate cuticle. As a result there is almost certainly a large amount of concealed convergence which is, as yet, unrecognized so that much of the current classification continues to be suspect.

DESCRIPTIVE SECTION

In agreement with the arguments of Wieser & Hopper (1967) I only give absolute measurements of specimens and have not given ratios.

Euchromadora striata (Eberth, 1863), Filipjer, 1918

(Text-figs. 12-24; 91-93)

Weed and associated hold-fasts and sand; silty and sheltered. In 60 cm. water. Cheyne Beach, Nr. Albany, W.A.

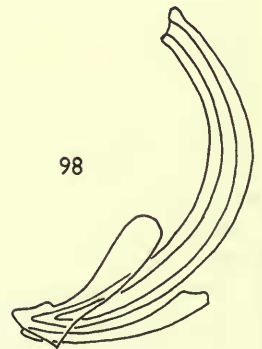
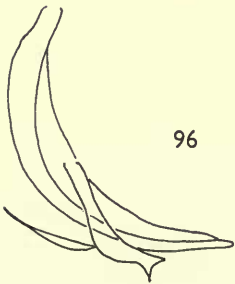
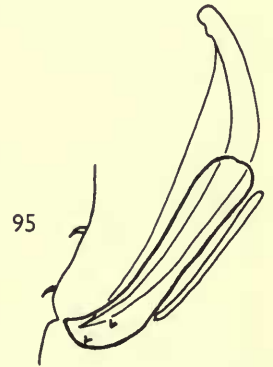
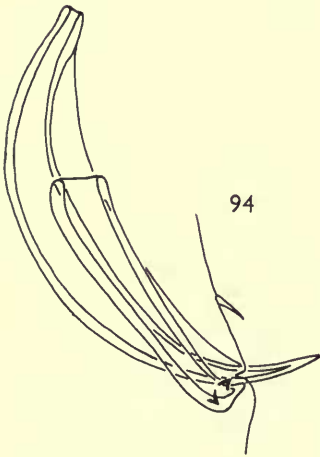
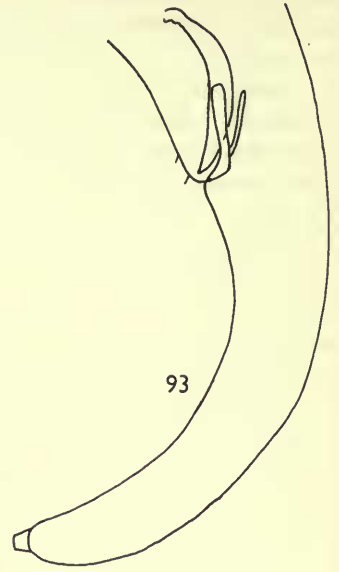
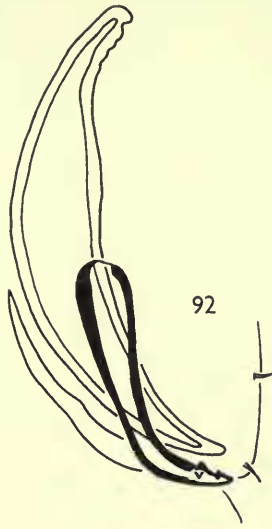
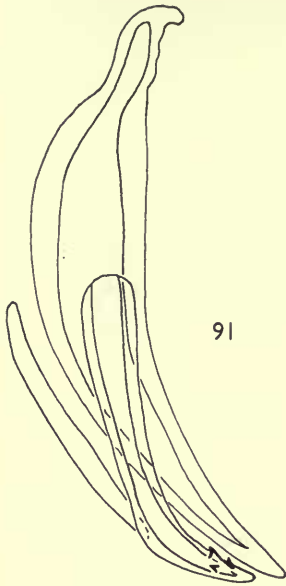
Weed and associated hold-fasts and sand; on exposed rocks. Goode Beach, Albany, W.A.

Weed and associated hold-fasts and sand; no silt, on exposed beach in 60 cm. water. Sarge Bay, Cape Leeuwin, W.A.

Among weed in rock pools. Robert Point, Mandurah, W.A.

Among weed on coral reef in 60 cm. water. Radar Reef, Rottneest Island, W.A. measurements (mm.).

MALES. Body length: 1.61; 1.64; 1.67; 1.86; 2.37. Body breadth: 0.078; 0.078, 0.076; 0.068; 0.082. Diameter of head: 0.031; 0.030; 0.033; 0.033; 0.033. Length of cephalic setae: 0.009; 0.010; 0.011; 0.011; 0.011. Oesophagus length: 0.31; 0.33; 0.33; 0.35; 0.36. Length of spicules: 0.075; 0.083; 0.085; 0.085; 0.079. Gubernaculum length; 0.052; 0.047; 0.052; 0.048; 0.046. Tail length: 0.185; 0.238; 0.232; 0.212; 0.215. Cloacal diameter: 0.066; 0.057; 0.061; 0.052; 0.059.



FEMALES. Body length: 2.13; 2.16; 2.63. Body breadth: 0.110; 0.098; 0.131. Diameter of head: 0.036; 0.036; 0.037. Length cephalic setae: 0.013; 0.011; 0.013. Oesophagus length: 0.40; 0.39; 0.43. Tail length: 0.208; 0.221; 0.234. Distance of vulva from anterior end: 1.18; 1.09; 1.25. Size of eggs: 0.069 × 0.046; 0.073 × 0.063.

This species is the same as that described by Coles (1965) and Filipjev (1918) and it should be noted that Coles' figure of the spicules (Fig. 26) shows the spicules as rather too narrow posteriorly and the "serrated" posterior end to the lateral piece of the gubernaculum is three denticles (Text-figs. 91, 92) as in the Australian specimens.

The only major differences between the specimens from Australia and England are that the setae are slightly shorter in the Australian forms. The detailed structure of the head is described on page 162.

This species is wide-spread and common on the coasts of Western Australia and I have collected it from as far north as Perth, south down the coast to Cape Leeuwin and along the south coast as far as Cheyne Beach about 30 miles east of Albany.

Euchromadora eileenae sp. nov.

(Text-figs. 31-37; 94-95)

Weed on coral in 60-100 cm. water; Radar Reef, Strickland Bay, Rottneet, W.A. (Type locality).

Weed and sand brought up in trawl from 12 m.; Shark Bay (midway between Denham and Dirk Hartog Island), W.A.

Weed and sand associated with hold-fasts, silty, sheltered, in 60 cm. water. Cheyne Beach, Nr. Albany, W.A.

Measurements (mm.)

MALES. Body length: 1.63; 1.79; 1.96; 2.05. Body breadth: 0.048; 0.064; 0.062; 0.059. Diameter of head: 0.023; 0.026; 0.026; 0.024. Length of cephalic setae: 0.008; 0.009; 0.009; 0.008. Length of oesophagus: 0.269; 0.281; 0.316; 0.296. Spicule length: 0.049; 0.053; 0.058; 0.061. Gubernaculum length: 0.034; 0.035; 0.040; 0.038. Tail length: 0.225; 0.189; 0.221; 0.236. Cloacal diameter: 0.039; 0.043; 0.041; 0.044.

FEMALES: Body length: 1.74; 1.87; 1.93. Body breadth: 0.093; 0.089; 0.091. Diameter of head: 0.026; 0.029; 0.029. Length of cephalic setae: 0.009; 0.009; 0.10. Length of oesophagus: 0.310; 0.314; 0.326. Tail length: 0.188; 0.208; 0.223. Anal diameter: 0.039; 0.040; 0.043. Distance of vulva from anterior end of body: 0.88; 0.91; 0.97. Diameter of eggs (spherical): 0.047-0.049.

FIGS. 91-98. 91-93. *Euchromadora striata*. 91-92. Gubernaculum and spicules. 93. Lateral view of male tail. 94-95. *Euchromadora eileenae*. Gubernaculum and spicules. Difference in appearance due to different angles of view. 96. *Graphonema georgei*. Gubernaculum and spicules. 97-98. *Parapinnanema wilsoni*. 97. Anterior end of body. Black region is thick cuticle in section. 98. Gubernaculum and spicules.

The structure of the head is described on page 162 and the cuticle is typical of the genus. The lateral plates are tiny and a series of four files of longish setae occur over the oesophageal region of the body.

The lateral pieces of the gubernaculum are stout with a very slight ventral curve at the distal end. On this curved region are two tiny denticles. The spicules are slightly curved and bear alae. This detail of both the spicules and the gubernaculum has been confirmed by dissection and is difficult to establish from whole mounts.

E. eileenae differs from all other members of the genus in the shape of the lateral pieces of the gubernaculum in which the distal end is hardly L-shaped.

The species is fairly common on the coasts of Western Australia with a wide range from Shark Bay in the north to Cheyne Beach in the east, on the south coast.

Parapinnanema wilsoni gen. et sp. nov.

(Text-figs. 51-55; 66-72; 73-75; 97-98)

From weed and associated sand without silt, on exposed beach in 60 cm. water. Sarge Bay, Cape Leeuwin, W.A. (Type locality).

From among finger-like green algae in rock-pools, just east of Cape Naturaliste (Bunker Bay), Geographe Bay, W.A.

Measurements (mm.).

MALES. Body length: 1.34; 1.47; 1.50; 1.78. Body breadth: 0.039; 0.034; 0.044; 0.046. Head diameter: 0.016; 0.016; 0.016; 0.018. Length of cephalic setae: 0.007; 0.007; 0.008; 0.006. Oesophagus length: 0.23; 0.24; 0.29; 0.27. Length of spicules: 0.041; 0.040; 0.039; 0.046. Length of gubernaculum: 0.023; 0.024; 0.022; 0.026. Length of tail: 0.143; 0.153; 0.148; 0.151. Cloacal diameter: 0.038; 0.047; 0.042; 0.041.

FEMALES. Body length: 2.34; 2.76. Body breadth: 0.073; 0.069. Head diameter: 0.023; 0.026. Length of cephalic setae: 0.006; 0.007. Oesophagus length: 0.42; 0.46. Length of tail: 0.257; 0.261. Anal diameter: 0.047; 0.049. Size of eggs: 0.053 × 0.042.

The structure of the head and of the cuticle is described on pages 171, 175 but it may be stressed that this species is easily recognized in collections by the extreme thickness of the cuticle over the oesophageal region of the body (Text-fig. 97).

The spicules are evenly curved, without proximal swellings or alae and terminate distally in sharp points. The lateral pieces of the gubernaculum are fairly broad and L-shaped. The short, distal arm of the gubernaculum carries a slight bulge on its inner surface which can be difficult to see on whole specimens but is immediately obvious on dissection. There is a median raised region of the cuticle anterior to the cloacal opening.

This species cannot be confused with any other because of the features diagnostic of the genus *Parapinnanema* (page 175). The discovery of further species referable to that genus must be awaited before a more restricted diagnosis can be established.

Graphonema georgei sp. nov.

(Text-figs. 80-84; 96; 99)

Weed and associated sand in hold-fasts on exposed rocks, Goode Beach, Albany W.A.

Measurements (mm.).

MALES. Body length: 1.30; 1.42. Body breadth: 0.052; 0.044. Diameter of head: 0.014; 0.014. Oesophagus length: 0.187; 0.198. Length of cephalic setae; intermediate/outer: 0.0026/0.0040; 0.0026/0.0040. Spicule length: 0.039; 0.043. Gubernaculum length: 0.017; 0.017. Tail length: 0.150; 0.164. Cloacal diameter: 0.036; 0.039.

The structure of the head is described above (page 180) and that of the cuticle on page 178. It may be stressed that the species is easily recognized by the swollen anterior end, the relatively posterior position of the amphids, the intermediate and the outer circles of setose cephalic sense organs, and the rather thin and delicate appearance of the cuticle.

The spicules are equal in length and identical in structure, fairly massive in appearance with narrow alae and slightly barbed posterior ends. The lateral pieces of the gubernaculum are relatively small and are a slightly curved L-shape (Text-fig. 96). The tail is long and slim and there is no pre-cloacal thickening on the mid-ventral surface of the body (Text-fig. 99).

The only other species referred to this genus is *G. vulgaris* Cobb, 1898 which is described without illustrations. All the cephalic setae are described as lying relatively near the anterior end of the body, while in the specimens from Western Australia they are far posterior to the same level. This difference could be because Cobb studied specimens in which the head was somewhat contracted but this appears unlikely as he refers to a number of papillae (eighteen) near the border of the mouth opening. These I interpret as the rugae which surround the mouth opening and the fact that they could be seen implies that the mouth was not fully closed.

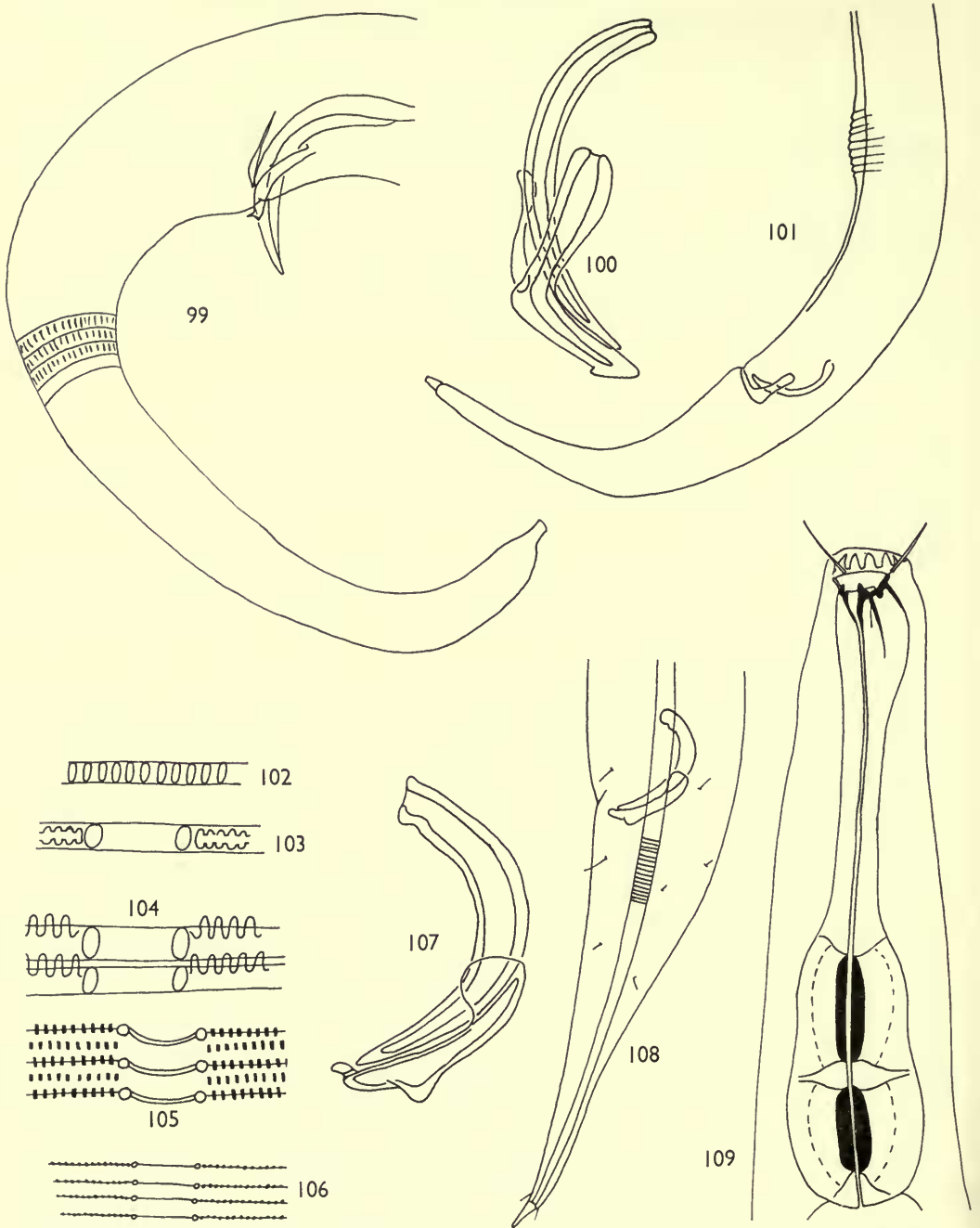
Cobb describes the spicules as ". . . of uniform size throughout, and are twice as long as the anal body diameter." while in the Western Australian specimens the spicules narrow markedly towards their extreme posterior ends and are about one cloacal width in length.

As a result of these differences I propose to treat the specimens from Western Australia as a distinct, new species, *G. georgei* sp. nov.

Austranema alii (Murphy, 1965) comb. nov.

(Text-figs. 38-40; 100-101)

Weed and sand from trawl from 12 metres in Shark Bay, W.A.; midway between Dirk Hartog Island and Denham.



FIGS. 99-109. 99. *Graphonema georgei*. Lateral view of male tail. 100-101. *Austranema alii*. 100. Gubernaculum and spicules. Fig. 101. Lateral view of male tail. 102-109. *Hypodontolaimus slacksmithi*. 102-106. Surface appearance of cuticle. 102. Between cephalic setae and anterior end of lateral differentiation. 103. Anterior end of lateral differentiation. 104. At anterior end of oesophageal bulb. 105. At posterior end of oesophagus. 106. At level of cloacal opening. 107. Gubernaculum and spicules. 108. Male tail. 109. Oesophagus.

Measurements (mm.).

MALES. Body length: 1.70; 1.78; 2.16. Body breadth: 0.052; 0.046; 0.057. Head diameter: 0.016; 0.017; 0.019. Setae length: 0.005; 0.005; 0.005. Oesophagus length: 0.22; 0.24; 0.27. Spicule length: 0.044; 0.038; 0.052. Gubernaculum length: 0.026; 0.021; 0.035. Pre-cloacal supplement, length/distance anterior to cloacal opening: 0.048/0.098; 0.034/0.091; 0.047/0.130. Tail length: 0.19; 0.19; 0.22. Cloacal diameter: 0.038; 0.033; 0.049.

FEMALES. Body length: 1.90; 2.31. Body breadth: 0.051; 0.057. Head diameter: 0.019; 0.021. Setae length: 0.004; 0.005. Oesophagus length: 0.27; 0.32. Tail length: 0.19; 0.21. Anal diameter: 0.033; 0.037. Vulva from anterior end: 0.90; 1.06. Size of eggs: 0.089 × 0.033; 0.074 × 0.036.

The spicules are equal and identical (Text-fig. 100). The lateral pieces of the gubernaculum are L-shaped with each arm about the same length. The distal end of the gubernaculum is slightly pointed and bears a slight notch on the under edge near the tip. There is a median pre-cloacal ventral modification in the form of a raised region of the cuticle. The three or four cuticular projections which ". . . appear to form a kind of bursa . . ." (Murphy, 1965, page 207) are due to the dense annules within the cuticle at the level of the cloacal opening projecting above the general body surface. This is because the cloacal opening itself is surrounded by an unannulate region and the projections represent the outer border of this region.

There are distinct granules lying on the lateral surface of the body between the annules, in a position corresponding to the lateral plates in *Euchromadora* species.

A. alii differs from the other species referred to the genus most particularly in the notched distal end to the lateral pieces of the gubernaculum and in the characteristic shape of the spicules.

Hypodontolaimus slacksmithi sp. nov.

(Text-figs. 56-59; 102-109)

Sand and weed brought up in trawl from 12 m.; Shark Bay, midway between Dirk Hartog Island and Denham, W.A. (Type locality).

Weed and hold-fasts on rocky flat in 12 cm. water; Cowaramup Bay, W.A.

Measurements (mm.).

MALES. Body length: 1.34; 1.46. Body breadth: 0.051; 0.052. Length of cephalic setae: 0.020; 0.022. Diameter of head: 0.036; 0.038. Length of oesophagus: 0.19; 0.23. Length of spicules: 0.039; 0.044. Length of gubernaculum: 0.030; 0.031. Length of tail: 0.13; 0.15; Cloacal diameter: 0.033; 0.042.

FEMALES. Body length: 1.38; 1.43. Body breadth: 0.075; 0.080. Length of cephalic setae: 0.021; 0.022. Diameter of head: 0.033; 0.037. Length of oesophagus: 0.22; 0.24. Distance of vulva from anterior end of body: 0.57; 0.63. Length of tail: 0.14; 0.17. Anal diameter: 0.039; 0.041.

The cuticular markings consist of prominent ovoid punctations just posterior to the cephalic setae (Text-fig. 102) and remain like this until the lateral differentiation

begins about half-way along the oesophagus length. Here the lateral differentiation, which is raised above the general surface of the body, consists of a bar flanked by large dots in turn flanked by battlement-like punctations which occur on both sides of the annules (Text-fig. 103). By the level of the anterior end of the oesophageal bulb, the lateral markings have become wholly battlement-like along the anterior edge of each annule. At the posterior end of the oesophagus, the lateral bars of the differentiation are narrow, the large dots flanking them are relatively small and the markings outside these again are now in the form of small, squarish punctations of which one row is level with the large dots of the lateral differentiation while one row lies between the large dots (Text-figs. 104-105). The punctations continue to become simpler posteriorly and less prominent until by the level of the cloaca or anus they consist of rows of small dots while the lateral differentiation consists of a clear strip flanked by a series of punctations which are only very slightly larger than those found elsewhere on the surface of the body (Text-fig. 106). There appear to be four files of ventro- and dorso-lateral setae on the body but they are small and indistinct.

The mouth opening is bounded by twelve lobes, without rugae, which are supported by twelve flanges of the cheilorhabdion. These flanges project inwards and over the cavity of the cheilostome as rather hook-like structures in optical section. The cephalic sense organs consist of two circles of six papillae and an outer circle of four long setae. The amphid was not seen but the head is set-off from the body. The tail narrows fairly rapidly and ends in a long, pointed spinnerette.

The oesophastome contains a very large, hollow dorsal onchium with a prominent dorsal apophysis in the male. The dorsal side of the oesophastome is very thick and slightly irregular in optical section longitudinally (Text-fig. 59). There is a lateral flange on each lateral wall of the retangular oesophastome, in *en face* view, which is highest towards the ventral side, and there is a single cone-like, anteriorly directed onchium on each ventro-lateral sector (Text-figs. 57-59).

The oesophagus ends posteriorly in a very prominent double bulb with a prominent cuticular lining (Text-fig. 109), of which the anterior bulb is slightly smaller than the more posterior.

The spicules are evenly curved and taper posteriorly to finely rounded ends. The gubernaculum is about two-thirds of the length of the spicules and is prominent with anterior, lateral processes which lie over the spicules laterally. There is a pair of slight bumps near the distal end of the gubernaculum on the side away from the spicules (Text-fig. 107).

This species is referable to the subgenus *Ptycholaimellus* Cobb, 1920 of the genus *Hypodontolaimus* de Man, 1888 as recognized by Gerlach (1955) and as followed by Wieser & Hopper (1967). It would probably be better to treat the group as a full genus, if it is to be recognized at all. There is little value in recognizing subgenera within free-living marine nematodes since they simply add another name to be considered.

Be that as it may, *H. slacksmithi* is, therefore, similar to *H. carinatus* Cobb, 1920; *H. poncticus* Filipjev, 1922; *H. pandispiculatus* Hopper, 1961 and *H. macrodentatus* Timm, 1961, from all of which it differs in the relatively stout, smoothly curved spicules and the massive gubernaculum.

SUMMARY OF GENERA AND SPECIES RECOGNIZED

Given here are brief summaries of the major diagnostic characters of the genera recognized and lists of the species referred to them. All genera are referred to the family Chromadoridae *sensu lato*.

EUCHROMADORA de Man, 1886

Head blunt with outer four sense organs setae; amphids without surrounding cuticular fringe; dorsal onchium solid; rows of denticles on lateral and ventral walls of oesophastome; oesophagus without posterior bulb; cuticle complex, unmarked dorsally and ventrally, not markedly thick over oesophageal region; lateral plates always present; no pre-cloacal modifications on male; tail short and stout.

Species:

E. vulgaris (Bastian, 1865); *E. gaulica* Inglis, 1962; *E. meadi* Wieser & Hopper, 1967; *E. permutabilis* Wieser, 1954; *E. tokiokai* Wieser, 1955; *E. striata* (Eberth, 1863); *E. eileenae* sp. nov.

STEINERIDORA gen. nov.

Generally similar to *Euchromadora*; differs in massive squarish dorsal onchium and sickle-like prominent onchia laterally and ventrally; oesophagus with posterior bulb; cuticular markings always about same size over full length of body laterally.

Species:

S. loricata (Steiner, 1916); *S. adriatica* (von Daday, 1901); *S. archaica* (Steiner & Hoeppli, 1926); *S. (?) dubia* (Steiner, 1918) sp. inq.

PARAPINNANEMA gen. nov.

Head set off as narrow region because of very thick cuticle over oesophagus length of body; intermediate circle of sense organs six setae and outer four setae; amphids with surrounding fringe of cuticle; dorsal onchium hollow; flanges on lateral walls and onchia ventrally in oesophastome; oesophagus without posterior bulb; cuticle very thick over oesophagus region and very battlement-like; cuticle with punctations dorsally and ventrally; tail long and slim; raised region of pre-cloacal modification on male.

Species:

P. wilsoni sp. nov.

PROTOCHROMADORA gen. nov.

Slim with rounded head; outer sense organs setae; dorsal onchium difficult to classify but frequently hollow looking; no elaborations on lateral walls of oesophastome but single onchium on each ventral sector; oesophagus without posterior bulb; amphid without cuticular fringe; cuticle not markedly thick over oesophageal

region; cuticle complex (?) without punctations dorsally and ventrally; tail short and stout; no pre-cloacal modification.

Species:

P. scampae (Coles, 1965); *P. mediterranea* (Allgén, 1942); *P. parafricana* (Gerlach, 1958).

GRAPHONEMA Cobb, 1898

Head set off as swollen, bulb-like region; cephalic sense organs in three well separated circles, outer of four setae and intermediate of six setae; amphid relatively far posterior on head, with cuticular fringe; dorsal onchium small and hollow; lateral flanges and ventral onchia in oesophastome; oesophagus without posterior bulb; cuticle fairly thin with distinct annulations and punctations; tail long and slim; no pre-cloacal modification on male.

Species:

G. vulgaris Cobb, 1898; *G. georgei* sp. nov.; *G. amokurae* (Ditlevsen, 1921).

INNOCUONEMA gen. nov.

Dorsal onchium hollow; with associated dorsal swelling of oesophageal musculature; outer circle of cephalic sense organs setae; amphid not prominent; posterior oesophageal bulb present; cuticle complex; tail long and slim; no pre-cloacal modification on male.

Species:

I. flaccida (Wieser, 1959); *I. clovosa* (Wieser, 1959); *I. tentabunda* (de Man, 1890); *I. chilensis* nom. nov.

NYGMATONCHUS Cobb in Cobb, 1933

Cuticle complex anteriorly, elongate punctations posteriorly; lateral differentiation present; intermediate and outer circles of cephalic sense organs setae; dorsal onchium hollow; amphid with prominent double contour (?); no posterior oesophageal bulb; tail long and slim with pre-cloacal modification(?).

Species:

N. scriptus Cobb in Cobb, 1933; *N. fossiferus* Wieser, 1954; *N. bicornata* (Wieser, 1959) comb. nov.; *N. minutus* Gerlach, 1967.

AUSTRANEMA gen. nov.

Head not set off or blunt; dorsal onchium difficult to classify but generally hollow and anteriorly directed; outer and intermediate cephalic sense organs in one circle of ten setae; flanges laterally and onchia ventrally in oesophastome; oesophagus without posterior bulb, although expanded evenly posteriorly; cuticle complex,

marked dorsally and ventrally, and thickened over oesophagus region; tail long and thin; pre-cloacal mid-ventral modification present on males.

Species:

A. colesi (Inglis, 1968); *A. shirleyae* (Coles, 1965); *A. alii* (Murphy, 1965); *A. pectinata* (Wieser & Hopper, 1967).

LIST OF NOMENCLATURAL CHANGES PROPOSED

Chromadora

- paraheterophya* Allgén, 1932 = *species dubia*
sabangensis Steiner, 1915 = *species inquirenda*
spectabilis Allgén, 1932 = *species dubia*
suilla Allgén, 1947 = *species dubia*
tentabunda de Man, 1890 = *Innocuonema t.* comb. nov.

Dicriconema

- tenuis* Steiner & Hoeppli, 1926 = *species inquirenda*

Euchromadora

- archaica* Steiner & Hoeppli, 1926 = *Steineridora a.* comb. nov.
arctica Filipjev, 1946 = *incertae sedis*
colesi Inglis, 1968 = *Austranema c.* comb. nov.
denticulata Cobb, 1914 = *species inquirenda*
dubia Steiner, 1915 = *Steineridora (?) d.* comb. nov.
hupferi Steiner, 1918 = *species dubia*
inflatispiculum Schuurmans
 Stekhoven, 1943 = *incertae sedis*
mediterranea Allgén, 1947 = *Protochromadora m.* comb. nov.
meridiana Cobb, 1914 = *species inquirenda*
parafricana Gerlach, 1958 = *Protochromadora p.* comb. nov.
pectinata Wieser & Hopper, 1967 = *Austranema p.* comb. nov.
scampae Coles, 1965 = *Protochromadora s.* comb. nov.
shirleyae Coles, 1965 = *Austranema s.* comb. nov.
stateni Allgén, 1930 = *species dubia*

Graphonema

- amokuroides* Wieser, 1954 = *Innocuonema chilensis* nom. nov.
clovosa Wieser, 1959 = *Innocuonema c.* comb. nov.
flaccida Wieser, 1959 = *Innocuonema f.* comb. nov.

Neochromadora

- bicornata* Wieser, 1959 = *Nygmatochus b.* comb. nov.

Nygmatochus

- alii* Murphy, 1965 = *Austranema a.* comb. nov.

Odontocricus

- hupferi* Steiner, 1918 = *species dubia*

Pareuchromadora

- fragilis* Allgén, 1942 = *species dubia*
setifer Schuurmans Stekhoven, 1943 = *species inquirenda*

Spilophora

- adriatica* v. Daday, 1901 = *Steineridora a.* comb. nov.
amokuræ Ditlevsen, 1921 = *Steineridora a.* comb. nov.
amokuroides Allgén, 1927 = *species dubia*
loricata Steiner, 1916 = *Steineridora l.* comb. nov.
norvegica Allgén, 1932 = *species dubia*
pusilla Allgén, 1947 = *species dubia*

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Hypodontolaimus slacksmithi is named in appreciation of Mr. Slack-Smith's efforts on my behalf; *Euchromadora eileenæ* is a small token of appreciation for Miss Mitchell's endurance in sorting formalin samples while *Austranema wilsoni* and *Graphonema georgei* are named in honour of Dr. B. R. Wilson and Dr. R. W. George respectively, W.A. Museum for the many kindnesses shown to me by them and their families during my stay in Perth, W.A.

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